

ANATOMY OF GUAYANA MUTISIEAE³⁰

SHERWIN CARLQUIST

I. Pollen.

Certain Mutisieae from the Guayana Highland described by Maguire, Wurdack and collaborators (1957) are remarkable for their unusual growth forms and distinctive morphological features. These genera show an equally interesting diversity when viewed from an anatomical standpoint. Because of the very primitive expressions of characters and severe modifications, they form one of the more critical areas of the Compositae for an understanding of evolution within this family, where anatomical characters appear to be particularly important in suggesting relationship and evolution. Pollen characters represent one facet of the striking variation found within the genera of Guayana Highland Mutisieae considered here.

Material for this study was obtained almost exclusively from the collections of the New York Botanical Garden, made on expeditions described by Maguire, Cowan and Wurdack (1953). For making this material available, the writer wishes to express his sincere appreciation to Dr. Bassett Maguire. Additional specimens, designated here as (GH) were provided through the courtesy of the Gray Herbarium. Grateful acknowledgement is also offered to Dr. I. W. Bailey and Dr. Reed C. Rollins for reading the manuscript and offering helpful suggestions.

METHODS

Because the quantity of pollen obtainable from some specimens was necessarily limited, a series of slides was prepared by making mounts of pollen grains without special treatment. This process consisted of spreading pollen grains from soaked anthers of herbarium material on slides coated with Haupt's adhesive, dehydrating in an ethyl alcohol series, straining with 1 per cent safranin in absolute ethyl alcohol, destaining, transferring to xylene, and using a xylene-soluble resin ("Damar") as a mounting medium. In most instances, a duplicate set of slides was prepared using pollen of flowers cleared in 5 per cent sodium hydroxide. Little difference either in size or detailed structure could be observed as a result of these two methods, and both seemed reliable for the purposes of the present study. Sectioned material of cleared flowers, prepared by means of conventional paraffin techniques and stained with safranin and fast green, was useful for confirming certain details of structure of pollen grains.

Dimensions of pollen grains and exine strata were obtained from fully turgid grains, as evidenced by bulging germ pores. Less turgid grains tend to show greater length (polar axis) and diminished width (equatorial axis). Since variability in size within a species could not be explored (in some species the information on size and morphology was necessarily derived from a single flower), it seemed best to obtain average dimensions from as many grains as showed proper turgidity and maturity and could be measured with certainty. While variation in size obviously exists, the figures given below will serve at least to indi-

³⁰Figures and footnotes in this paper are numbered consecutively with those of "Botany of the Chimantá Massif" (Mem. N.Y. Bot. 9:393-439).

Table 1. Dimensions of Pollen of Mutisieae.

	polar axis, μ	equatorial axis, μ	approximate spine length, μ	width endexine, μ^*	width inner exine, μ^*	width outer exine, μ^*	total width exine, μ^*	total width exine, polar, μ
<i>Stenopadus</i>								
<i>campestris</i> , Maguire 35573	60	60	1-2	1	2	1.5	4.5	5
<i>chimantensis</i> , Steyermark & Wurdack 652	62	46	1	1	1	1.5	3.5	4.5
<i>connellii</i> , Wurdack 34265	65	47	< 1	1	1.5	1	3.5	4.5
<i>cucullatus</i> , Maguire & Maguire 35120	58	59	< 1	1	1.5	2	4.5	4.5
<i>huachamacari</i> , Maguire et al. 30012	50	41	1	1	1	3	5	5.5
<i>kunhardtii</i> , Maguire & Politi 27896	60	50	< 1	1	2	.5	3.5	3.5
<i>obconicus</i> , Maguire et al. 37077	55	44	1	1	1	1.5	3.5	4.5
<i>sericeus</i> , Maguire 33415	57	45	< 1	1	1	1	3	4
<i>Stomatochaeta</i>								
<i>condensata</i> , Maguire 40603	48	36	< 1	1	1	1	3	3.5
<i>crassifolia</i> , Cowan & Wurdack 31162	46	35	< 1	1	1	1	3	3.5
<i>cylindrica</i> , Maguire 32782	49	35	< 1	1	1.5	1.5	4	4
<i>cymbifolia</i> , Steyermark & Wurdack 508	51	37	< 1	1	1	1	3	4.5
<i>Chimantaea</i>								
<i>cinerea</i> , Cardona 2717	59	40	1-2	1	1.5	2	4.5	4.5
<i>espeletoidea</i> , Steyermark & Wurdack 574	56	47	1	1.5	1.5	1.5	4.5	4.5
<i>lanocaulis</i> , Steyermark 57912	51	47	1	1	1.5	2	4.5	5.5
<i>mirabilis</i> , Steyermark & Wurdack 821	63	48	2	1	1	1.5	3.5	4
<i>rupicola</i> , Steyermark & Wurdack 748	57	46	1-2	1	2	1.5	4.5	4.5
<i>similis</i> , Steyermark & Wurdack 605	58	47	1	1	2.5	1.5	5	5
<i>Quelchia</i>								
<i>bracteata</i> , Steyermark & Wurdack 754	52	45	2-3	2	3.5	3	8.5	9
<i>cardonae</i> , Steyermark & Wurdack 565	53	47	2	2	3	3	8	7.5
<i>conferta</i> , Pinkus 112	56	44	2	1	3.5	3.5	8	8
<i>× grandifolia</i> , Steyermark & Wurdack 755	50	48	2	2	3	3	8	
<i>Stiffia</i>								
<i>chrysantha</i> , Trin. Bot. Gard. 1330 (GH)	77	66	1	1	3	3.5	7.5	8-9
<i>uniflora</i> , Schultes 4719 (GH)	54	44	1-2	1	1.5	2	4.5	3.5
<i>Gongylolepis</i>								
<i>bracteata</i> , Maguire 37560	78	78	4	2.5	5	4	11.5	12
<i>fruticosa</i> , Steyermark & Wurdack 1136	55	55	2	2	2	3.5	7.5	7.5
<i>huachamacari</i> , Maguire et al. 30262	73	69	5	2	7	7	16.5	16.5
<i>martiana</i> , Schultes 14158 (GH)	85	83	4	3	5	5	13	12

*Optical section of equator, at middle of intercolpar area.

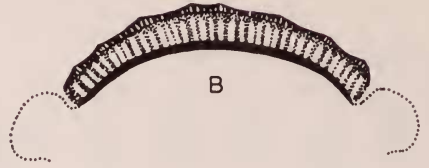
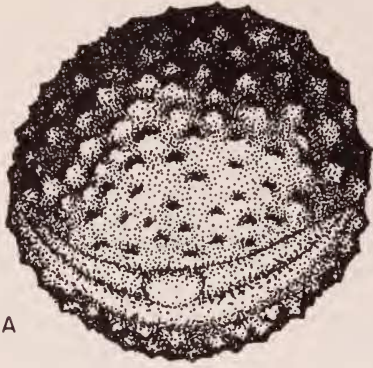
	polar axis, μ	equatorial axis, μ	approximate spine length, μ	width endexine, μ^*	width inner ektexine, μ^*	width outer ektexine, μ^*	total width exine, μ^*	total width exine, polar, μ
<i>paniculata</i> , Maguire & Maguire 35392	76	75	4	2.5	6.5	5	14	15
<i>paruana</i> , Maguire et al. 30256	65	64	3	2	6	4	12	12.5
<i>pedunculata</i> , Cowan & Wurdack 31131	79	80	4.5	3	6.5	5.5	15	12
<i>Achnopogon virgatus</i> , Steyermark & Wurdack 742	52	46	2	1.5	4	3	8.5	10
<i>Neblinaea promontorium</i> , Maguire et al 37016	50	40	1-2	2	3.5	3	8.5	8.5
<i>Duidaea pinifolia</i> , Steyermark 58143	55	50	3	1.5	3.5	4	9	9
<i>tatei</i> , Steyermark 58204	58	45	1	1.5	3	2.5	7	8.5
<i>Glossarion rhodanthum</i> , Maguire et al. 37190	56	52	2	2	3	3.5	8.5	7

cate some relatively prominent differences among the genera and species represented. In the data below, the length of spines is included in all measurements except endexine and inner ektexine thickness.

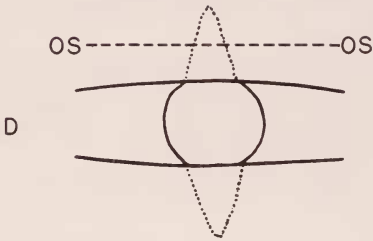
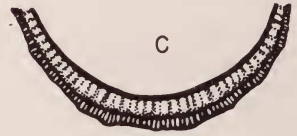
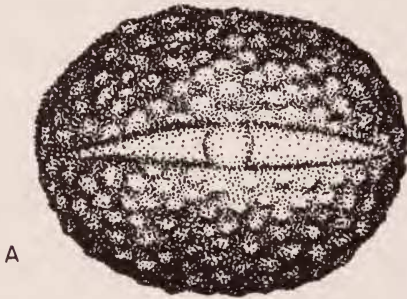
The terminology in this study is derived mostly from the lucid and graphic handbook of Faegri and Iversen (1950). As increasing knowledge of detailed structure of pollen has accumulated, new terms have been added to the literature; those of Faegri and Iversen seem the most practicable at the present moment. For descriptions of grain shape and spine length, the terms of Erdtman (1952) have been used.

DESCRIPTIONS

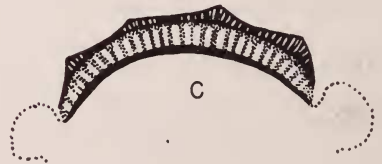
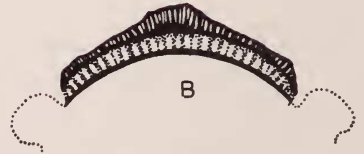
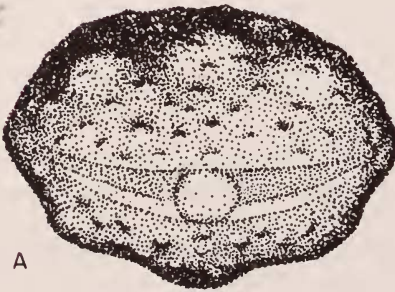
Several features are common to all the pollen grains of the genera discussed here. As the drawings of entire grains show, the three furrows on each grain are long and pointed, with the edges clearly defined. Optical sections, shown to the right in each plate, demonstrate the three-layered nature of the exine. The innermost of these layers, endexine (referred to by Erdtman as "nexine"), is unsculptured. Exterior to the endexine, and adherent to it, is the two-layered ektexine. The inner ektexine (termed "endosexine" by Erdtman), which is apparently continuous with the endexine and like it in staining properties, is composed of rods. These rods (called "bacula" by Erdtman) may be variously shaped and fused with each other, and are surrounded by a network of spaces apparently not filled by any solid material. Transections of this layer (i.e., sections tangential to the surface of the grain) may be seen in figures 95C, 96C, 98C, and 100C. The outer ektexine differs from the inner ektexine in its staining properties and finer



89



90



91

structure. Outer ektexine may be seen to contain extremely fine striae or chambers which are often at the limit of visibility of the light microscope. Since the finer structure of the exine in Mutisieae has been little studied to date, the pattern described above has not been previously reported for this group, although the drawings of Erdtman (1952) for *Mutisia speciosa* suggest it.

Variations in the thickness of the exine layers may be seen within an individual pollen grain, although the relative thickness of layers, as seen at an arbitrarily chosen plane of section, is a character of taxonomic importance. An example of variation in thickness of exine layers within a single pollen grain is seen for *Stenopadus hauchamacari* in figure 90. In this pollen grain, the ektexine layers show a greater thickness at the poles of the grain. As a comparison of the measurements in table 1 shows, this difference is found in a number of the genera considered here. The thickness of the exine may be approximately constant within a grain, however, with differential prominences of each layer at various places in the grain. In *Stomatochaeta cylindrica* (fig. 92 B, C), for example, the endexine and outer ektexine are thicker, the inner ektexine thinner, at the poles than at the equator. In *Stomatochaeta condensata* (fig. 92 D), the inner ektexine is so narrowed at the poles that no sculpturing could be seen in that layer, although the outer ektexine is quite conspicuous.

Although differences in polar versus equatorial thickness are not present in all species, a transverse furrow (fig. 90 D, E), caused by a thinning in the endexine, was seen in all species. This furrow is adjacent to the germ pore and runs at right angles to the colpa. The shape of this transverse furrow, as shown in figure 90D, was relatively constant for all the taxa investigated. This structure was found by Wodehouse (1929 a, b) in many of the Mutisieae he studied.

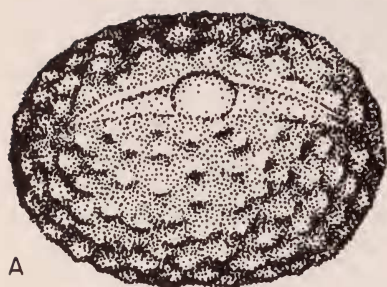
The genera below are arranged in two main groups. Those of the first (*Stenopadus* through *Wunderlichia*) have actinomorphic flowers and belong to the subtribe Gochnatinae. In the remaining genera, with the exception of *Glossarion*, the corolla form is exclusively bilabiate (Gerberinae). In *Glossarion* the corollas are ligulate in form.

Stenopadus.

With the exception of *S. campestris*, the species of *Stenopadus*, as exemplified by *S. chimantensis* fig. 90 A, B), have the following characters in common. The grains have an elliptic outline, this shape being described by Erdtman (1952) as subprolate for those of narrower shape, or prolate sphaeroidal for those approaching more nearly a sphaeroidal form. The outer ektexine is virtually smooth (psilate), the spinulose emergences being one micron or less high. *Stenopadus campestris* (fig. 89 A, B) shows a sphaeroidal shape, with minute spines (spinulose) somewhat larger than those in the other species. All species of *Stenopadus* show a relatively thin exine, approximately 3 to 5 microns in thickness.

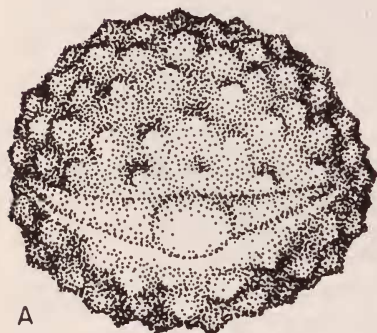
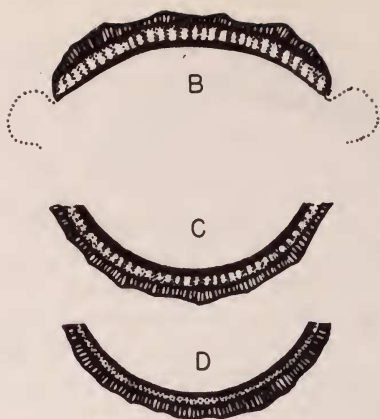
Explanation of Figures 89-91

FIG. 89. *Stenopadus campestris*; A, pollen grain; B, optical section of grain at equator (germ pores shown at right and left). FIG. 90. A, *Stenopadus chimantensis*, pollen grain; B, *S. chimantensis*, optical section of grain at equator; C, *S. huachamacari*, optical section of pole of grain; D, diagram showing portion of colpa of *S. chimantensis*, enlarged; transverse furrow is shown above and below germ pore by dotted lines; E, portion of exine in plane of optical section indicated by OS-OS in D. FIG. 91. A, *Stiffia chrysantha*, pollen grain; S, *chrysantha*, optical section of grain at equator; C, *Wunderlichia mirabilis* (Glaziou 2168G; GH), optical section of grain at equator. FIG. 90 D, E, $\times 1600$; 91 A, B, $\times 700$; all others, approximately $\times 800$. Specimens represented are indicated in table 1.



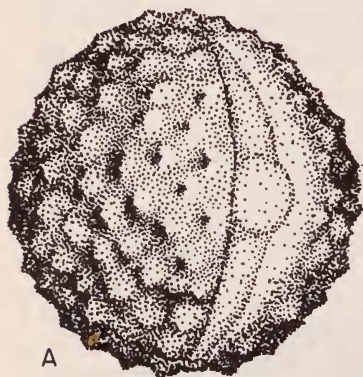
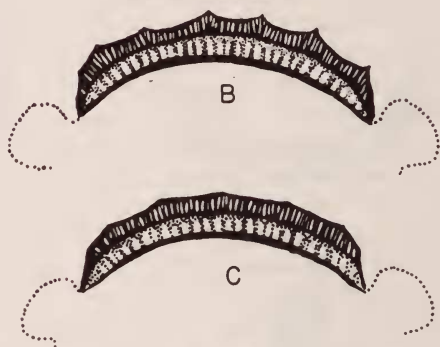
A

92



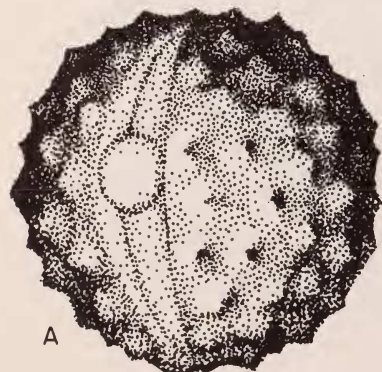
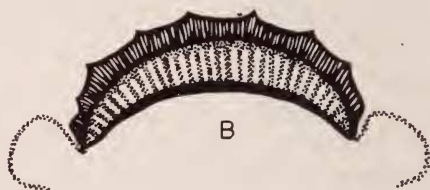
A

93



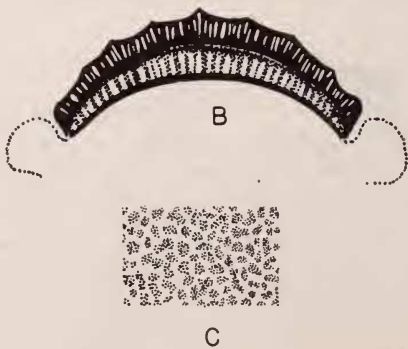
A

94



A

95



Stomatochaeta.

Pollen grains of the species of *Stomatochaeta* agree closely with those of *Stenopadus* other than *S. campestris*. As shown for *Stomatochaeta cylindrica* in figure 92 A-C, the grains are subprolate in shape. Furrows are shorter than in *Stenopadus*. The exine is psilate or nearly so, and exine thickness is approximately the same as in *Stenopadus*. Grains of *Stomatochaeta*, however, seem to be appreciably smaller than those of most species of *Stenopadus*.

Chimantaea.

Although not conspicuously different from those of the above genera, the pollen grains of *Chimantaea* have somewhat more prominent spines and greater exine thickness. While some species are spinulose, such as *C. rupicola* (fig. 93 A, B), others are more nearly psilate, such as *C. similis* (Fig. 93 C). The variation in shape of pollen grains is approximately that found in *Stenopadus*, ranging from subprolate to prolate sphaeroidal. In size, the pollen grains of *Chimantaea* also fall within the range found in *Stenopadus*.

Quelchia.

Pollen grains of *Quelchia* are easily separable from the above genera by virtue of the greater exine thickness and somewhat more prominent spines. *Quelchia barcteata* (fig. 94 A, B) is typical for the genus, as indicated by the material available. As shown in table 1, exine thickness and spine length are appreciably greater in *Quelchia*; in shape, however, the grains are subprolate to prolate sphaeroidal, like those of *Stenopadus*.

Stiffitia.

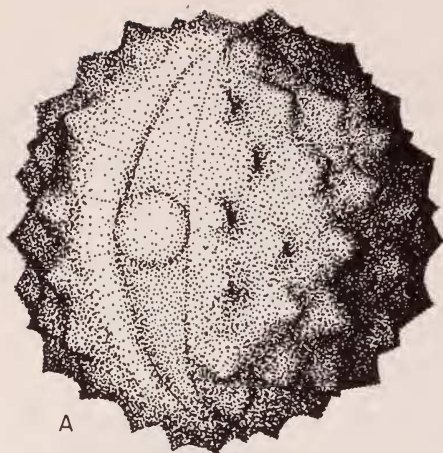
The genus *Stiffitia*, although not found on the Guayana Highland, shows some degree of relationship to the above genera and may be considered in this connection. The pollen grains of *Stiffitia chrysantha* (fig. 91 A, B) have a remarkable feature not previously reported for Mutisieae. Evenly arranged on the surface of these grains are eleven areas of thickened exine, three on each intercolpar face and one at each pole. These thickenings are the result of greater development of the outer ectexine (fig. 91 B). Numerous wide but very short spines or emergences occur on the thickened areas of the exine as well as on the unthickened areas. However, no such thickened areas are found on the pollen of *Stiffitia uniflora*, the grains being evenly spinulose. The pollen grains of *S. uniflora*, not illustrated here, would match closely the drawings of *Chimantaea rupicola* in figure 93 A, B. In shape, the pollen grains of these two species of *Stiffitia* are dissimilar, since *S. chrysantha* has large, subprolate grains, while those of *S. uniflora* are smaller and prolate sphaeroidal. Excepting the thickened areas in *S. chrysantha*, the exine thickness of these two species is very similar; likewise both have long, narrow furrows.

Wunderlichia.

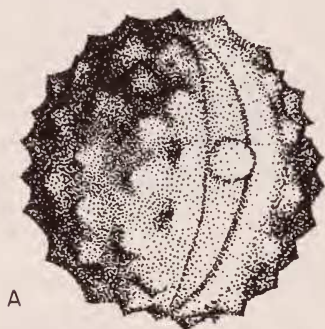
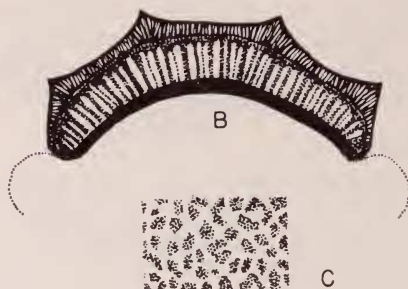
Before discussing the genera which have corollas bilabiate or ligulate in form, the genus *Wunderlichia* may be mentioned. As suggested by Wodehouse (1929 b),

Explanation of Figures 92-95

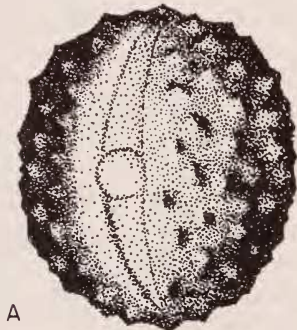
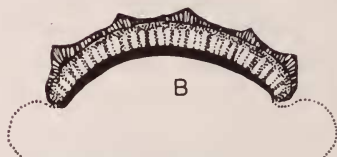
FIG. 92. A-C, *Stomatochaeta cylindrica*; A, pollen grain; B, optical section of grain at equator; C, optical section of grain at pole; D, *S. condensata*, optical section of grain at pole. FIG. 93. A, *Chimantaea rupicola*, pollen grain; B, *C. rupicola*, optical section of grain at equator; C, *C. similis*, optical section of grain at equator. FIG. 94. *Quelchia bracteata*; A, pollen grain; B, optical section of grain at equator. FIG. 95. *Glossarion rhodanthum*; A, pollen grain; B, optical section of grain at equator; c, section of inner ectexine tangential to grain surface. Figure 95 C, $\times 1000$. All others, approximately $\times 800$. Specimens represented are listed in table 1.



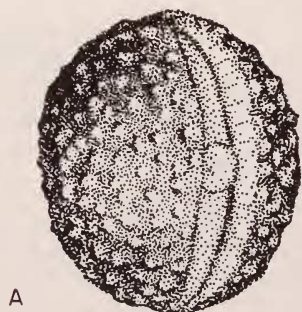
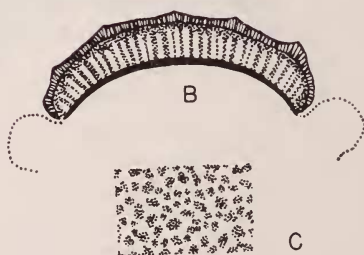
96



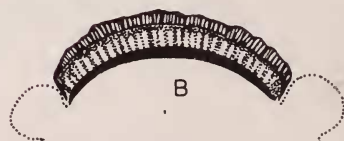
97



98



99



this genus represents an anomalous element in the subtribe Gochnatinae. An entire grain of *Wunderlichia mirabilis*³¹ has been illustrated by Wodehouse (1929 b). Although the furrows are somewhat shorter than in the genera considered here the exine sculpturing (shown in optical section, Fig. 91 C) is not markedly different from that of other genera in the present study. In terms of its structural characters, the pollen of *Wunderlichia* seems well within the range of the Gochnatinae considered in this paper. It is of interest to note that according to the measurements given for this species by Wodehouse, it is the only member of the Gochnatinae he investigated which matches in its dimensions the relatively large pollen grains characteristic of all the Gochnatinae in the present study.

Gongylolepis.

As the dimensions of table 1 and the drawings of *G. pedunculata* (fig. 96 A, B) show, most species of *Gongylolepis* are markedly different from all other taxa studied here. With the exception of *G. fruticosa*, all the species of *Gongylolepis* have larger grains, sphaeroidal in shape, with thicker exine and longer spines than pollen grains of the other genera. As seen in figure 96 B, the two layers of the ectexine are particularly well developed, the inner showing relatively large rods (seen in a section tangential to the grain, fig. 96 C). *Gongylolepis fruticosa* (fig. 97 A, B) has a decidedly diminished expression of these characters, but is still distinguishable from grains of other taxa of this study by virtue of the sphaeroidal shape and prominent spines.

Achnopogon.

The monotypic genus *Achnopogon* shows considerable similarity to *Gongylolepis* in its pollen grain structure. However, the grains are not sphaeroidal, the shape being best described as prolate sphaeroidal (fig. 98 A). As shown in figure 98 B, the thick exine, with a particularly prominent inner ectexine, is reminiscent of *Gongylolepis*. The rods of the inner ectexine (fig. 98 C) are smaller than those of the large-grained species of *Gongylolepis*. The spine dimensions are likewise smaller. Except for shape, pollen grains of *Achnopogon* are very close to those of *Gongylolepis fruticosa*.

Neblinaea.

Pollen grains of the monotypic genus *Neblinaea* (fig. 99 A, B) have a close affinity to those of *Gongylolepis* and *Achnopogon*. However, the spines are less prominent than in either of these genera, the grains being less markedly spinulose. As in *Achnopogon*, the shape of pollen grains of *Neblinaea* is prolate sphaeroidal. The exine is only slightly thinner than that of *Gongylolepis fruticosa*, the two layers of the ectexine being about equally prominent.

³¹The name used by Wodehouse, "*W. tomentosa*," is a nomen nudum. A comparison of plants distributed by Glaziov under this name (e. g. *Glaziov 2168G*) with the description of the type species of the genus, *W. mirabilis* Ried., seemingly reveals no appreciable differences (see, for example, Hook. Ic. pl. 1496). Pending a new treatment of the genus, these plants may be regarded as belonging to *W. mirabilis*.

Explanation of Figures 96-99

FIG. 96. *Gongylolepis pedunculata*; A, pollen grain; B, optical section of grain at equator; C, section of inner ectexine tangential to grain surface. FIG. 97. *Gongylolepis fruticosa*; A, pollen grain; B, optical section of grain at equator. FIG. 98. *Achnopogon virgatus*; A, pollen grain; B, optical section of grain at equator; C, section of inner ectexine tangential to grain surface. FIG. 99. *Neblinaea promontorium*; A, pollen grain; B, optical section of grain at equator. Figures 96C, 98C, $\times 1000$; all others, approximately $\times 800$. Specimens represented are listed in table 1.

Duidaea.

The distinctive genus *Duidaea* has pollen grains, in *D. pinifolia*, similar to those of *Gongylolepis*. Grains of *D. pinifolia* (fig. 100 A-C) are sphaeroidal and spinose, and have thick walls. Rods of the inner ektexine (fig. 100 C) are relatively small. No features other than those found in *Gongylolepis*, however, characterize *D. pinifolia*. The exine structure of *D. tatei* (fig. 101 A-C), therefore, is surprising. Large lobe-like thickenings are found in intercolpar and polar areas. These are distributed symmetrically, two on each intercolpar face and one on each pole. In terms of the layers of the ektexine, this thickening is chiefly reflected by a widening of the outer ektexine (fig. 101 C), although the inner ektexine is also thicker in these areas. In addition to these prominent emergences, numerous minute spines are present on the unthickened areas of the exine. Pollen of *D. tatei* is further distinguished from that of *D. pinifolia* in that the shape of the grains is basically subprolate.

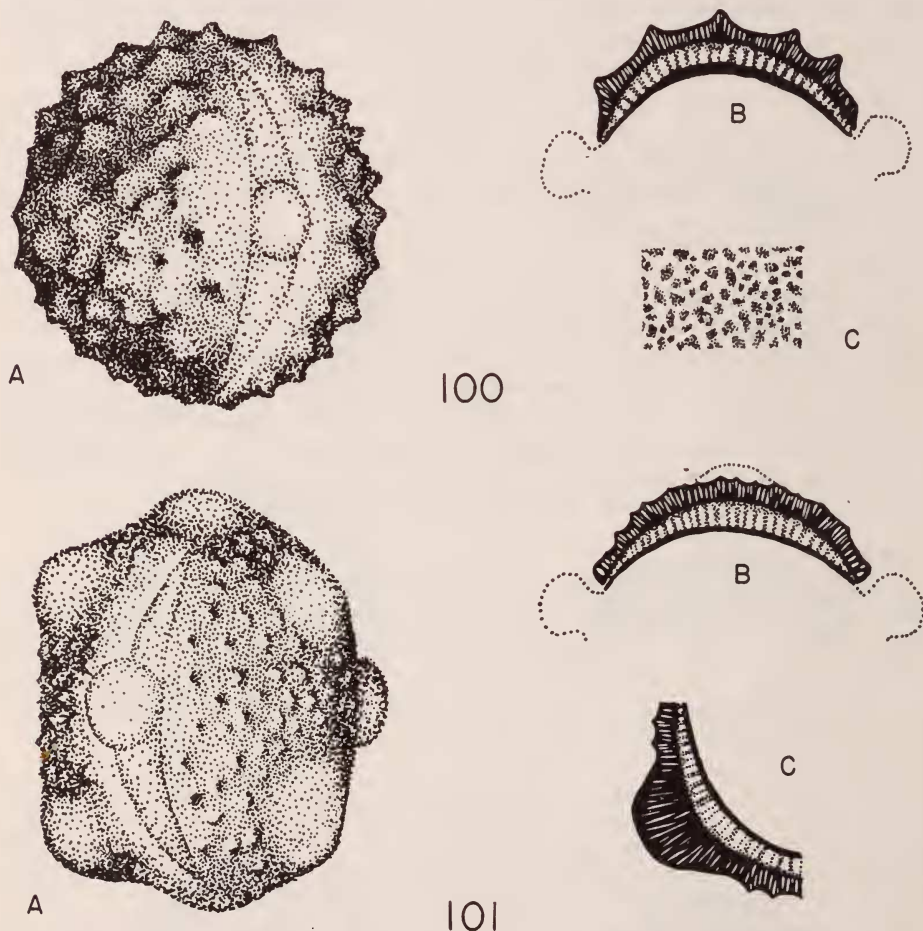


FIG. 100. *Duidaea pinifolia*; A, pollen grain; B, optical section of grain at equator; C, section of inner ektexine tangential to grain surface. FIG. 101. *Duidaea tatei*; A, pollen grain; a germ pore is shown at extreme right; B, optical section of grain at equator; dotted line, above, indicates outline of an intercolpar thickened area below the plane of the optical section; C, longitudinal optical section of grain, showing a thickened area such as is indicated at lower left in A. Figure 100, $\times 1000$. All others, approximately $\times 800$. Specimens represented are listed in table 1.

Glossarion.

Despite the anomalous corolla form of the monotypic genus *Glossarion*, pollen grains of this plant (fig. 95 A-C) are not unlike those of other genera considered here, since they have a sphaeroidal shape and bear short, broad spines. There is little conclusive evidence for placing *Glossarion* in the stenopadoid or gongylolepid line on the basis of pollen alone. The very fine pattern of the inner ectexine (fig. 95 C) resembles that of *Stenopadus* and its allies. Except for *Quelchia* and *Stiffitia*, however, none of those genera has such a thick exine. A feature not seen in pollen of any other genera studied here besides *Glossarion* is the possession of a third ectexine layer. This layer occurs between the two ectexine layers comparable to those found in the other pollen described (fig. 95 B). It was not possible to determine to which of these ectexine layers this deep-staining middle could be referred.

DISCUSSION

The facts presented above suggest some degree of generic differentiation in pollen grain structure and dimensions. Differences found among the stenopadoid genera in these respects correspond with the conclusions reached by Maguire (1956) and Maguire et al. (1957) on the basis of gross morphological study. *Stenopadus*, *Stomatochaeta*, and *Chimantaea* show great similarity in their pollen grains, differences being relatively minor; *Quelchia* pollen grains are easily distinguishable from the foregoing genera, though they show similarities. Also in agreement with the conclusions of Maguire and his coworkers are the resemblances in pollen grain structure found among the genera *Gongylolepis*, *Duidaea*, *Neblinaea*, and *Achnopogon*. The thick exine common to these genera is significant; minor differences in spine length and grain size parallel the generic lines.

The pollen grains of *Stiffitia* have many features of resemblance to those of *Stenopadus* and its allies. Taken as a group, pollen grains of all the genera discussed here illustrate a basic pattern upon which variations have taken place. In at least two genera (*Stiffitia* and *Duidaea*) species can be separated on pollen characters.

Since some of the Mutisieae considered here (particularly *Stenopadus*) demonstrate as large a constellation of primitive characters as may be found in the tribe, it is of interest to examine the pollen in this connection. On the basis of his work with various genera and species of Mutisieae, Wodehouse (1929 a) suggests that short furrows and a spinose exine are primitive in the tribe, and that the lengthening of furrows and the decreasing of spine size are indications of a phyletic advancement. The fact that all the genera in the present study (with the exception of *Stomatochaeta* and *Wunderlichia*) have very long furrows would seem to render Wodehouse's suggestion on furrow length open to question. Both long and short furrows occur in both putatively primitive and advanced Mutisieae, and this character may be of little importance phylogenetically. Likewise, while a spinose nature, variously expressed, is seen in virtually all Mutisieae, reduction to a psilate condition may occur within a single genus, as shown by Wodehouse (1929 b) in *Moquinia*. This character, then, may also be unreliable as a phylogenetic indicator.

In respect to pollen grain shape one would expect, on the basis of primitive Heliantheae, a sphaeroidal shape to be primitive. Both sphaeroidal and markedly elliptical pollen grains occur in areas of the Mutisieae which are not closely related. Most of the genera considered here show a close approach to the sphaeroidal condition, however, and the more markedly elliptical grains seem to indi-

cate a specialization. The very small and decidedly elliptical grains found by Wodehouse (1929 a) in *Trixis* and by Erdtman (1952) in *Mutisia* are likewise seemingly advanced.

The development of areas of thickened exine, seen here particularly in *Stiffitia chrysantha* and *Duidaeta tatei*, would seem to be an advanced character. Polar thickenings, such as those seen to a moderate extent in several of the genera considered in this paper, have been reported by Wodehouse (1929 a, b) for a number of genera of Mutisieae which are not regarded as being closely related. Polar thickenings, therefore, may represent a sporadic tendency within the tribe, and may perhaps be regarded as advanced, at least where most conspicuously expressed.

It is of interest to compare the two-layered ectexine in the Mutisieae with the condition found in the Heliantheae. In *Helianthus annuus* (illustrated by Erdtman, 1952) and other relatively primitive Heliantheae examined by the writer, a thick ectexine consisting of only a single layer but containing small lumina (largely restricted to the spine basis) is found exclusively. It seems apparent that the types of exine stratification found in putatively primitive Heliantheae and Mutisieae respectively represent two lines. Speculation concerning the relative primitiveness of these two patterns would not seem justified because of our extremely limited knowledge of this essentially cytological character. It is of interest, however, that the more complicated ectexine occurs in other tribes of Compositae, as an examination of the drawings of Erdtman (1952) will show.

II. Floral Venation

The genera of Guayana Highland Mutisieae treated taxonomically earlier in this series by Maguire et al. (1957) demonstrate a wide variety of floral venation patterns. Among these are the most complicated yet to be reported for the Mutisieae, and indeed, the most elaborate yet found in the Compositae at large. Since floral anatomy appears to be of considerable evolutionary significance within the Compositae, a description of these patterns seems desirable.

Herbarium material was used exclusively for these studies, and the kindness of Dr. Bassett Maguire in providing this material from the Herbarium of the New York Botanic Garden is gratefully acknowledged. Several additional specimens, designated here as (GH), were made available through the courtesy of the Gray Herbarium, Harvard University. For reading the manuscript and offering helpful suggestions, sincere appreciation is expressed to Dr. Reed C. Rollins and Dr. I. W. Bailey.

METHODS

Whole mounts of corollas, achenes, and styles were used to a large extent in determining venation. These were prepared by clearing in warm 2.5 per cent aqueous sodium hydroxide until most of the cellular contents had been removed; further clearing was achieved by prolonged treatment in 25 per cent aqueous chloral hydrate. After clearing, specimens were washed, dehydrated in an ethyl alcohol series, stained with a 1 per cent safranin solution in absolute ethyl alcohol, destained, transferred to xylene, and mounted in a xylene-soluble resin ("Damar"). Because achenes become sclerified upon maturation, obscuring venation, and because the disposition of interior and exterior bundles in the achene cannot be ascertained from clearings, serial sections of flowers were prepared to supplement information derived from the whole mounts. These were made by embedding cleared flowers according to the tertiary butyl alcohol series of Johansen (1940) and staining sections following Northen's modification of Foster's tannic acid-ferric chloride method (Johansen 1940).

DRAWING CONVENTIONS

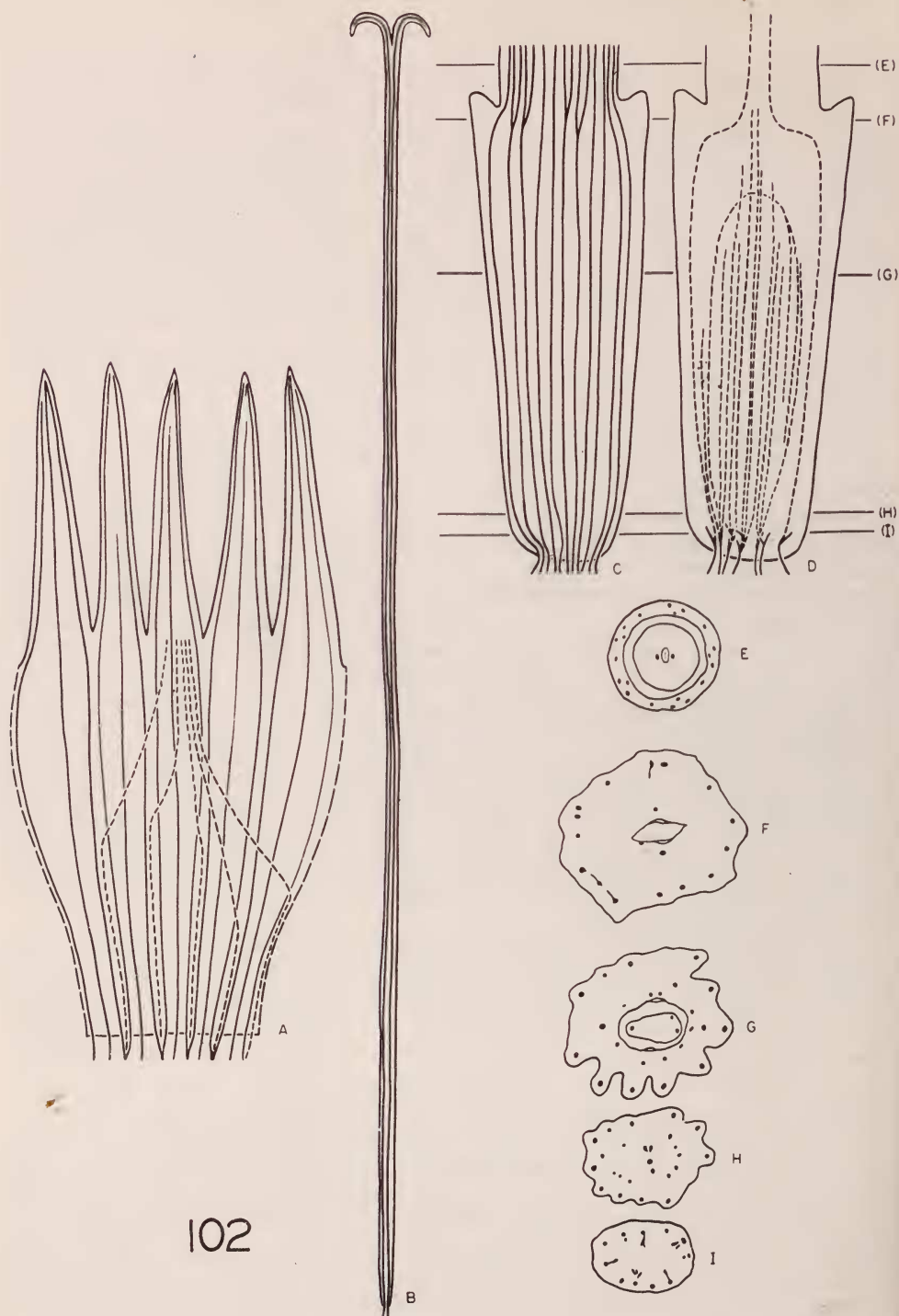
All the species in this study are discoid (although the flowers of *Glossarion* are ligulate in form from the standpoint of gross morphology). The accompanying drawings of floral parts, therefore, represent the venation of a particular disk flower. Although the parts of a flower have been separated for purposes of drawing, they may be interpreted as being intercontinuous. This separation was necessary because of the great complexity of venation. The proportions of the parts and the locations of veins within them reflect as accurately as possible the actual condition in the material studied, but an effort has been made to render the drawings simpler by avoiding the crossing of bundles over one another, such as is seen when viewing a given preparation of a style or achene. In species where variable numbers of lesser veins may be found in flowers, a more complicated flower is usually represented, and simpler conditions, if they were found to occur, are described in the text.

The corollas, which appear first in each figure, are shown to be cut the length of the tube and spread flat. This cut, which corresponds to the manner in which whole mounts of corollas were prepared, is made slightly to one side of the adaxial sinus of the corolla tube, and is indicated by the portion of the corolla outline drawn in lines broken at wide intervals. Stamen traces are indicated by lines broken at narrow intervals. Because stamen traces may vary in length depending on the state of development of the flower, they are of interest only in respect to the point in the corolla tube at which they depart (indicated by a curving away from the adjacent veins) and in respect to their union with corolla veins (mostly in the achene, just beneath the base of the corolla). For reasons of simplification, stamen traces are not shown in the drawings of entire achenes, but they are shown in the transection of the corolla base in each figure.

Styles and achenes are viewed laterally, i.e. in the position in which they would be seen in a radial section of a head. Thus the two stigmatic branches at the apex of a style, which are disposed adaxially and abaxially, are shown at right and left in each drawing. Bundles of the style which continue into the achene are extended beyond the outline of the style. The styles drawn do not include the nectary, which would be beneath the base of the style in the taxa in which a nectary is present.

The Mutisieae investigated in this study have two series of bundles in the achene. The exterior bundles are connected above with veins of the corolla or terminate freely in the top of the achene; the interior bundles are continuous with the style bundles or terminate freely in the upper portion of the achene. These two series of bundles are considered to represent perianth and carpellary bundles respectively, and a distinction is consequently made. The exterior bundles of the achene are shown in unbroken lines; the interior bundles and ovule trace are represented by broken lines. In many of the drawings, these two sets of bundles are shown in complementary pairs of drawings, because to show both of them in a single drawing would be too complicated. Since the style bundles are a continuation of the interior bundles, they are shown in broken lines in the achene drawings. Where the two sets of bundles are separate, portions of the exterior bundles are shown on the carpellary bundle drawing if interior bundles connect with them, and may be distinguished from the interior bundles since they are drawn in unbroken lines. Portions of the bundle or bundles which extend from the achene into the receptacle are shown in order to indicate the nature of vascular connections between these two structures.

A series of selected transections, starting from the corolla base and going to the achene base, is shown for most of the figures. This series is intended to show the disposition of exterior and interior bundles, and to aid in interpreting



102

FIG. 102. *Stenopadus campestris* (Maguire 35573), portions of flower drawn to show venation. A, corolla; B, style; C, achene, showing exterior bundles; D, achene showing interior bundles; E-I, successive sections of the corolla base and achene at levels indicated by (E) to (I) above. A, B, $\times 4.5$; C-I, $\times 9$. Further explanation of conventions in text.

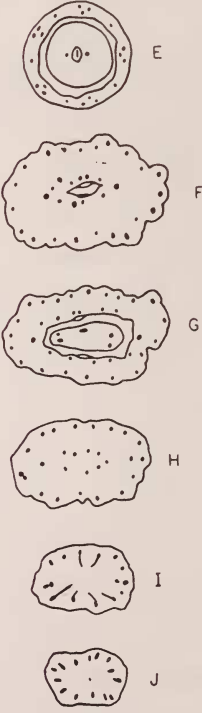
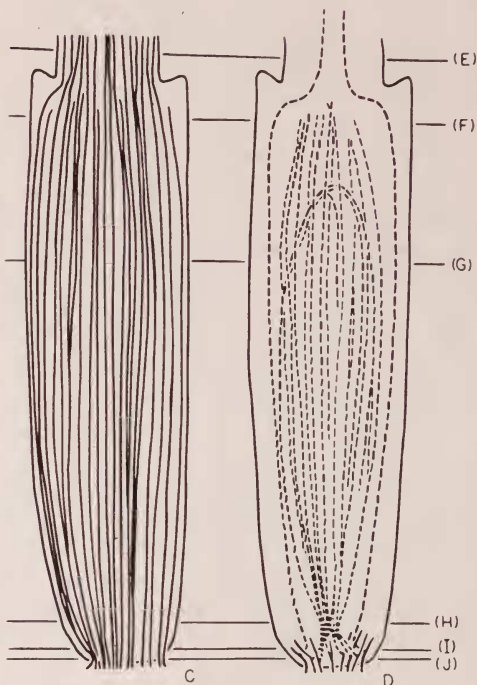
the drawings of entire achenes. In these sections, the outlines of the corolla and nectary (or style base) are shown, and for the achene, those of the achene wall and ovule. The two strands of stigmatic tissue, which occur as fused bands in the style, separating to lateral positions on the inner face of the achene wall (rejoining at the base of the achene cavity and running toward the micropyle) are shown as variously shaped ellipses in these drawings.

The terms "vascularization" and "venation" in this study refer only to xylem elements, unless phloem is specifically mentioned. In many bundles, the phloem is coincident with the xylem. It should be understood, however, that this is by no means always the case. In achenes particularly, strands of phloem may be present without any accompanying xylem. Such strands may be found as internal bundles in the achene. In addition, they interconnect bundles in the achene top. In species in which the xylem of stamen traces was not seen to connect with other bundles at the base of stamen traces, phloem elements could often be seen to interconnect these bundles. In all species, strands of phloem, connecting to bundles at the achene top, branch to form an anastomosing network in the nectaries. This phloic vascularization of nectaries has been described for certain Compositae by Frei (1955) and need not be detailed here. In many of the taxa studied here, phloem strands could be seen to branch from exterior achene bundles at the achene top and terminate freely at the base of pappus bristles. The addition of phloic bundles to the vasculature drawings would have made them complex beyond interpreting, and would have added no critical features not also exhibited by xylem. Phloem has therefore been omitted in the drawings and xylem is used as the prime indicator of the vascular pattern of the flower.

DESCRIPTIONS

Stenopadus.

This genus demonstrates the most elaborate floral venation yet found in Compositae. A basic but by no means typical situation is found in *Stenopadus campestris* (fig. 102). In the corolla of this species (fig. 102A), a pair of lateral veins is found in each lobe. These extend from the tips of the lobes to the base of the corolla; adjacent laterals fuse in the achene top, not in the corolla itself. Occasionally (fig. 102 C, extreme right), adjacent laterals do not fuse but remain separate in the achene. In addition to the laterals, median veins are present in each lobe. Median veins extend for various distances into the corolla lobes. If they do not extend to the tip, they terminate freely, as do the laterals; if they do extend to the tip, they join with one of the laterals at the tip. Median bundles extend into the achene, where they continue as five of the exterior bundles (fig. 102 C). The xylem of stamen traces terminates freely in the top of the achene or joins with that of corolla bundles. In details of venation, the corolla of *S. campestris* resembles that found in *Fitchia speciosa* of the Heliantheae (Carlquist 1957b). The style of *S. campestris* (fig. 1 B) is vascularized by a pair of dorsiventrally arranged bundles; these continue into the achene (fig. 102 D), joining two of the exterior bundles on opposite sides of the achene base. In addition, numerous other interior bundles are present in the achene. At the achene base, a lateral pair of these join with the ovule trace for a short distance (fig. 102 H), separating below to join exterior bundles, as do the remainder of the interior bundles (fig. 102 I). Thus, there are approximately ten bundles arranged in a cylinder passing from the achene base into the receptacle. The ovule trace (fig. 102 D, G) branches dichotomously in the chalaza, and the adaxial portion is double.



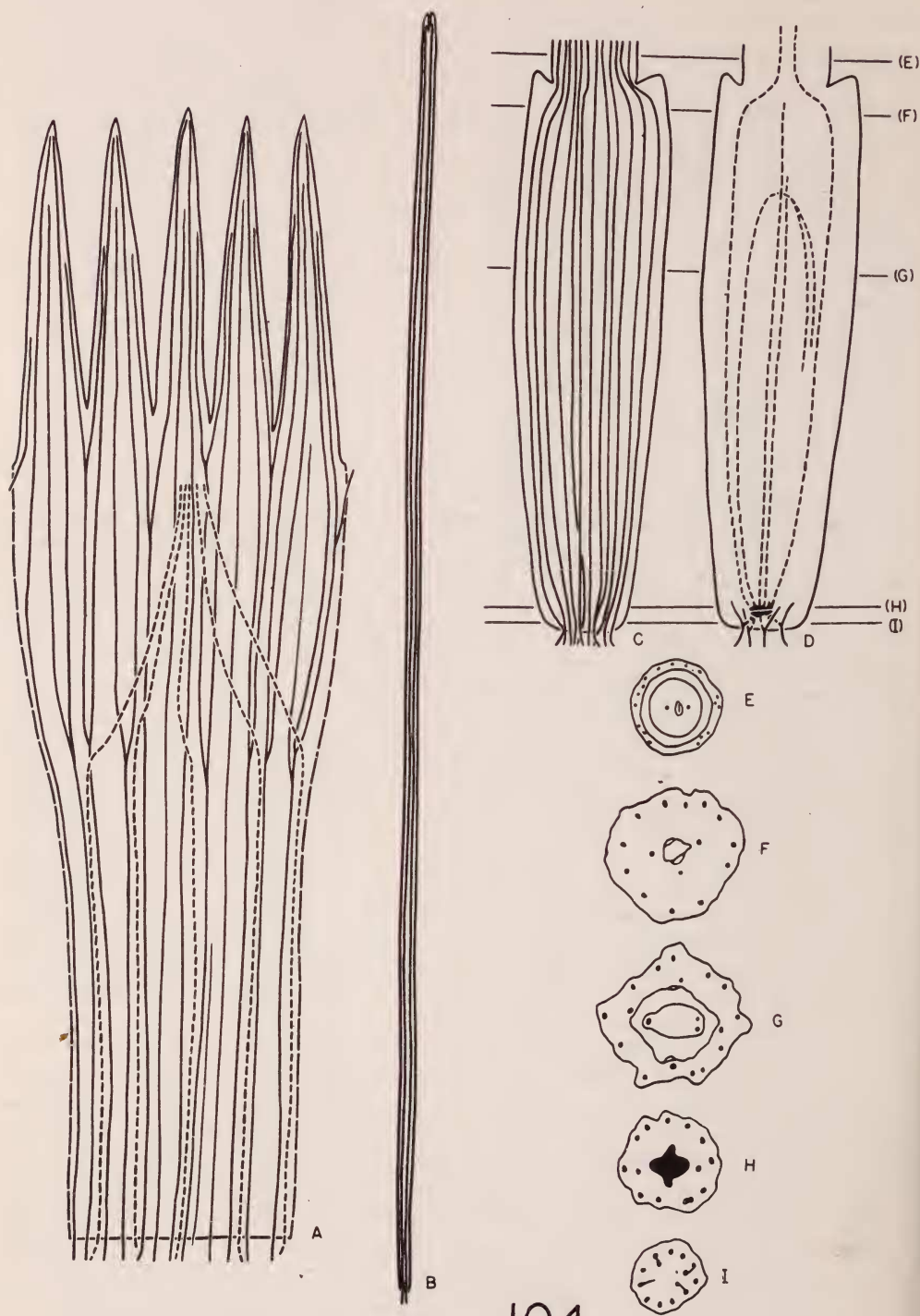
A somewhat more complex situation is represented by *Stenopadus kunhardtii* (fig. 103). In the corolla (fig. 103 A), lateral and median veins are present, as in *S. campestris*. In addition, subsidiary veins branch from the laterals at various points between the level of departure of stamen traces and the bases of the sinuses. These subsidiary veins occupy a position between the lateral veins and the margins of each lobe, and extend for various distances into the distal portion of the lobes, where they terminate freely. This pattern of corolla venation has been found elsewhere in the Compositae only in *Fitchia mangarevensis* (Carlquist 1957 a, b). At the base of the corolla of *S. kunhardtii*, the laterals continue into the achene, without fusion of adjacent laterals (fig. 103 C). Likewise, the five median veins of the corolla extend into the achene independently. The xylem of stamen traces terminates freely in the achene top. In the achene, more than the fifteen bundles continuous with those of the corolla are found. These additional exterior bundles (fig. 103 C) are branches of the fifteen corolla bundles. As in *S. campestris*, the style of *S. kunhardtii* contains two bundles (fig. 103 B) which connect with a dorsiventrally arranged pair of bundles in the achene (fig. 103 D). These connect with adjacent exterior bundles in the achene base (see also fig. 103 I, J). Numerous other interior bundles are present in the achene. These terminate freely above, but connect in a plexus with the ovule trace below, this plexus then separating to join several of the exterior bundles in the achene base (fig. 103 I). The ovule trace (seen also in fig. 103 G) is branched several times. At the base of the achene, a cylinder of bundles enters the receptacle.

In *Stenopadus stipitatus* (fig. 104), as in *S. kunhardtii*, there is a remarkably complex corolla vasculature (fig. 104 A). Because of the various ways in which the bundles unite, the designation of median, lateral, and subsidiary bundles cannot be made in *S. stipitatus*. The basic pattern of five bundles in each corolla-lobe seems evident, however. All bundles of the corolla-lobes terminate freely above. At the corolla base, as in *S. kunhardtii*, the bundles in the corolla tube pass into the achene without union of adjacent laterals (fig. 104 C). Xylem of most stamen traces terminates freely in the achene summit without coming in contact with that of the corolline bundles. As in the two above species, two style bundles are present (fig. 104 B, C, E). These are connected with a dorsiventral pair of interior achene bundles (fig. 104 D). In addition, a lateral pair of interior bundles is present; all four interior bundles, together with the ovule trace, form a vascular plexus at the achene base (fig. 104 H). This separates, further down, to form strands joining the exterior bundles (fig. 104 I). The ovule trace is dichotomous on the adaxial face of the ovule (fig. 104 G). As in the above species, a cylinder of bundles enters receptacular tissue.

In *Stenopadus cucullatus* (fig. 105), a much simpler corolla venation is found (fig. 105 A). Lateral bundles, which fuse at the apex of each corolla lobe, are present, but median veins are only occasionally present in lobes, and do not extend into the tubular portion of the corolla. As in *S. kunhardtii* and *S. stipitatus*, the lateral bundles enter the achene, without union of adjacent laterals, and form a series of external bundles (fig. 105 C). In the style (fig. 105 B), a pair of larger dorsiventrally arranged bundles is present; in addition, a lateral pair of small bundles extends part way up the style, fusing with the larger bundles.

Explanation of Figure 103

FIG. 103. *Stenopadus kunhardtii* (Maguire & Politi 27896), portions of flower drawn to show venation. A, corolla; B, style; C, achene, showing exterior bundles; D, achene, showing interior bundles; E-J, successive sections of corolla base and achenes at level indicated by (E) through (J) above. A, B, $\times 4.5$; C-J, $\times 9$.



104

FIG. 104. *Stenopadus stipitatus* (Maguire & Maguire 35358), portions of flower drawn to show venation. A, corolla; B, style; C, achene, showing exterior bundles; D, achene, showing interior bundles; E-I, successive sections of the corolla base and achene at levels indicated by (E) through (I) above. A, B, $\times 4.5$; C-I, $\times 9$.

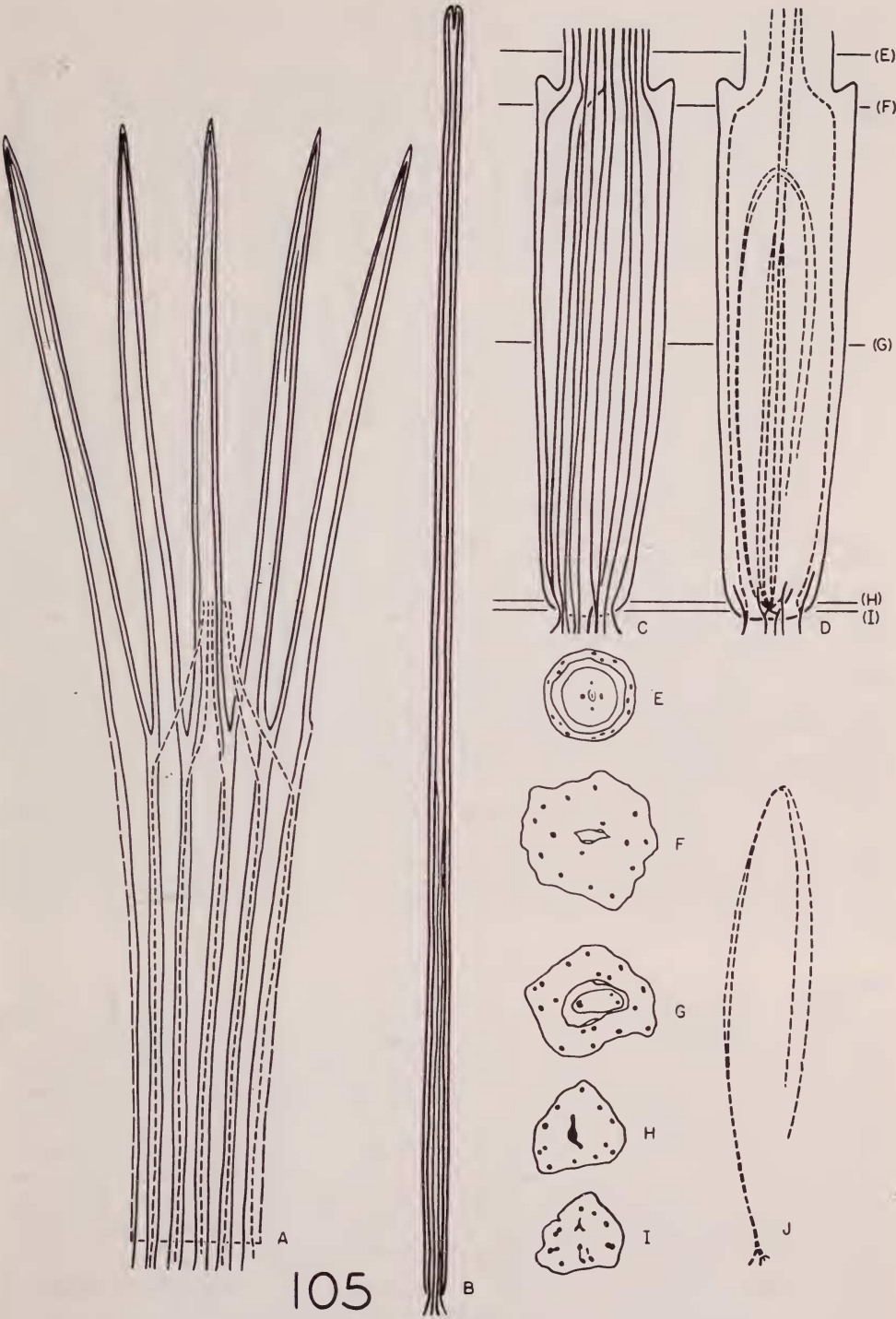


FIG. 105. A-I, *Stenopadus cucullatus* (Maguire & Maguire 35120), portions of flower drawn to show venation. A, corolla; B, style; C, achene, showing exterior bundles; D, achene, showing interior bundles; E-I, successive sections of the corolla base and achene at levels indicated by (E) through (I) above; J, *Stenopadus chimantensis* (Steyermark & Wurdack 652), ovule trace. A, B, $\times 4.5$; C-J, $\times 9$.

The four style bundles extend from the style into the achene (fig. 105 D) where they become interior bundles (fig. 105 F). The two lateral interior bundles branch in the lower half of the achene (fig. 105 G) so that they are double along part of their extent. The dorsiventral pair of interior bundles connect, at the achene base, with adjacent exterior bundles. The lateral interior bundles, together with the ovule trace, form a plexus (fig. 105 H) which separates lower down (fig. 105 I) to join exterior bundles. A cylinder of bundles connects with receptacle vascular tissue. The ovule trace is dichotomously branched (fig. 105 D, G). For comparison, an ovule trace of *S. chimantensis* is shown in figure 105 J. In the ovule studied of this species, the trace was dual in two places, although single at the base and at the chalaza.

Among the other species of *Stenopadus* for which material was available, *S. chimantensis*, *S. connellii*, *S. huachamacari*, *S. obconicus*, and *S. sericeus* were found to have corolla vasculature like that of *S. cucullatus*, though median bundles were entirely lacking in these species. Median bundles were found in the lobes, though not in the tube, of *S. colombianus* corollas. Two bundles were found in the styles of all of these species, and various numbers (though not fewer than four) interior bundles occurred in the achenes. Ovule traces may or may not be branched in these species. The frequency within the genus of various vascular conditions could not be ascertained from the material available. It is sufficient for the purposes of the present study, however, to note that certain conditions seemingly not present in the majority of mutisioids are prominently represented in *Stenopadus*. These features may be summarized as follows; median veins are present in the corolla in addition to lateral bundles (which branch to form subsidiary bundles in some species); the lateral bundles are not united in the corolla, and may or may not be united in the achene; xylem of stamen traces often terminates freely in the summit of the achene; at least 10 exterior bundles are present in the achene; two, sometimes four, style bundles continue into the achene as interior achene bundles; a dorsiventral pair of interior bundles is always present, and two to several lateral interior bundles are present in the achene; characteristic vascular configurations occur at the base of the achene, in all species forming a cylinder of independent bundles which enter receptacular tissue; the ovule trace is often dichotomously branched, though it may be further ramified or unbranched.

Stiffitia.

Before comparing these vascular patterns with the remainder of Guayana Mutisieae composing the basis for this study, a pertinent comparison can be made with the flowers of *Stiffitia chrysantha* (fig. 106), which is, like *Stenopadus*, a South American representative of the subtribe Gochnatinae. The corollas of this species (fig. 106 A), often have median veins in addition to the lateral veins; lateral veins do not fuse at the corolla-lobe tips. Median veins, where present, usually extend only part of the length of the corolla, terminating freely above, and only infrequently continuing to the base of the corolla tube. As in the vast majority of Compositae known, though not as in *Stenopadus*, adjacent laterals fuse beneath sinuses of the corolla in *Stiffitia chrysantha*. Thus, in the corolla shown, six bundles enter the achene. In addition to the six bundles in the achene continuous with those of the corolla, four others are present, forming a total of ten exterior bundles in the achene wall (fig. 106 C, F). Xylem of stamen traces joins with that of adjacent corolline bundles in the top of the achene. In the style (fig. 106 B) two bundles are present. These continue into the achene as interior bundles

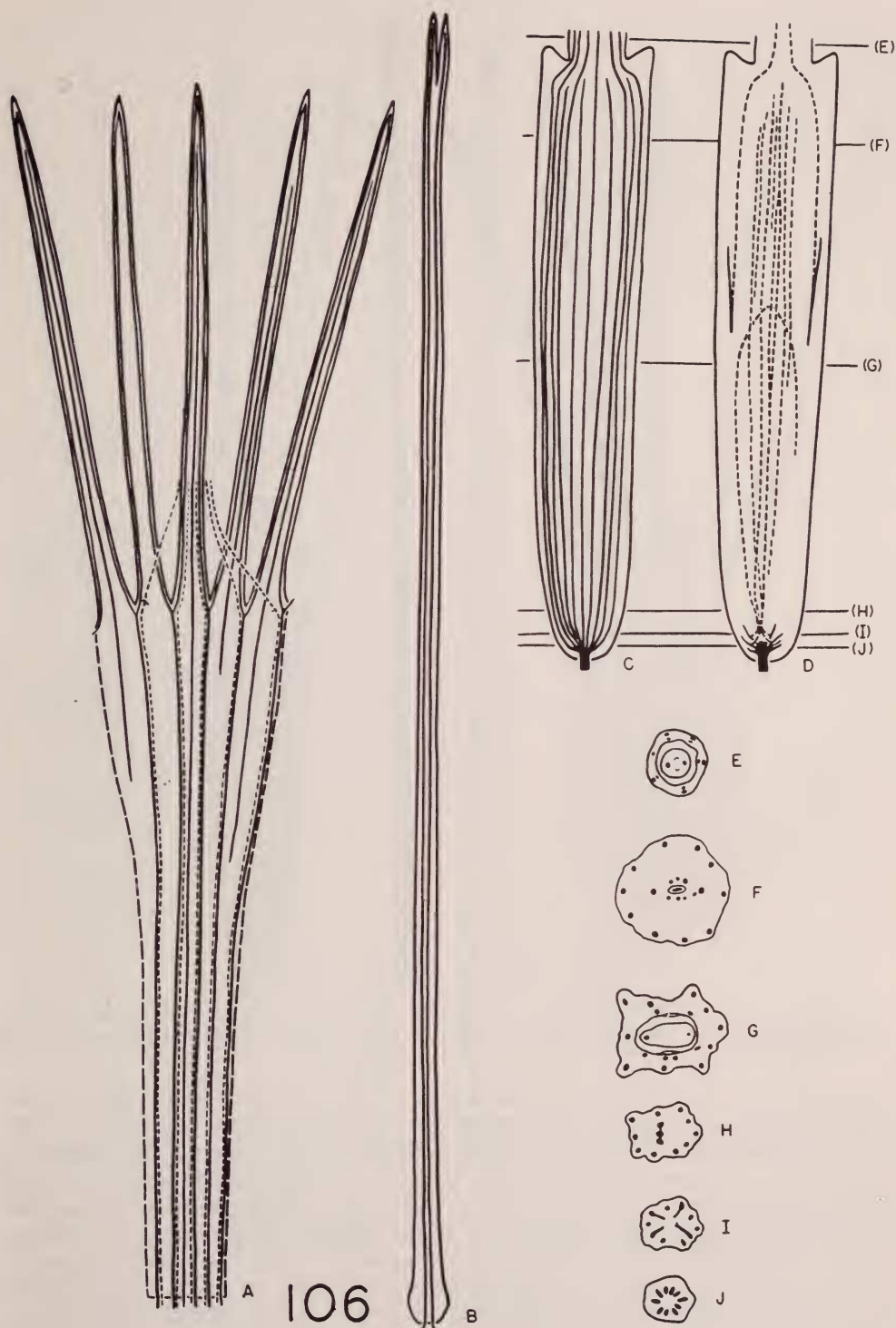


FIG. 106. *Stiffitia chrysantha* (Trinidad Botanic Garden 1330; GH), portions of flower drawn to show venation. A, corolla; B, style; C, achene, showing exterior bundles; D, achene, showing interior bundles; E-J, successive sections of corolla base and achene at levels indicated by (E) through (J) above. A, B, $\times 3$; C-J, $\times 6$.

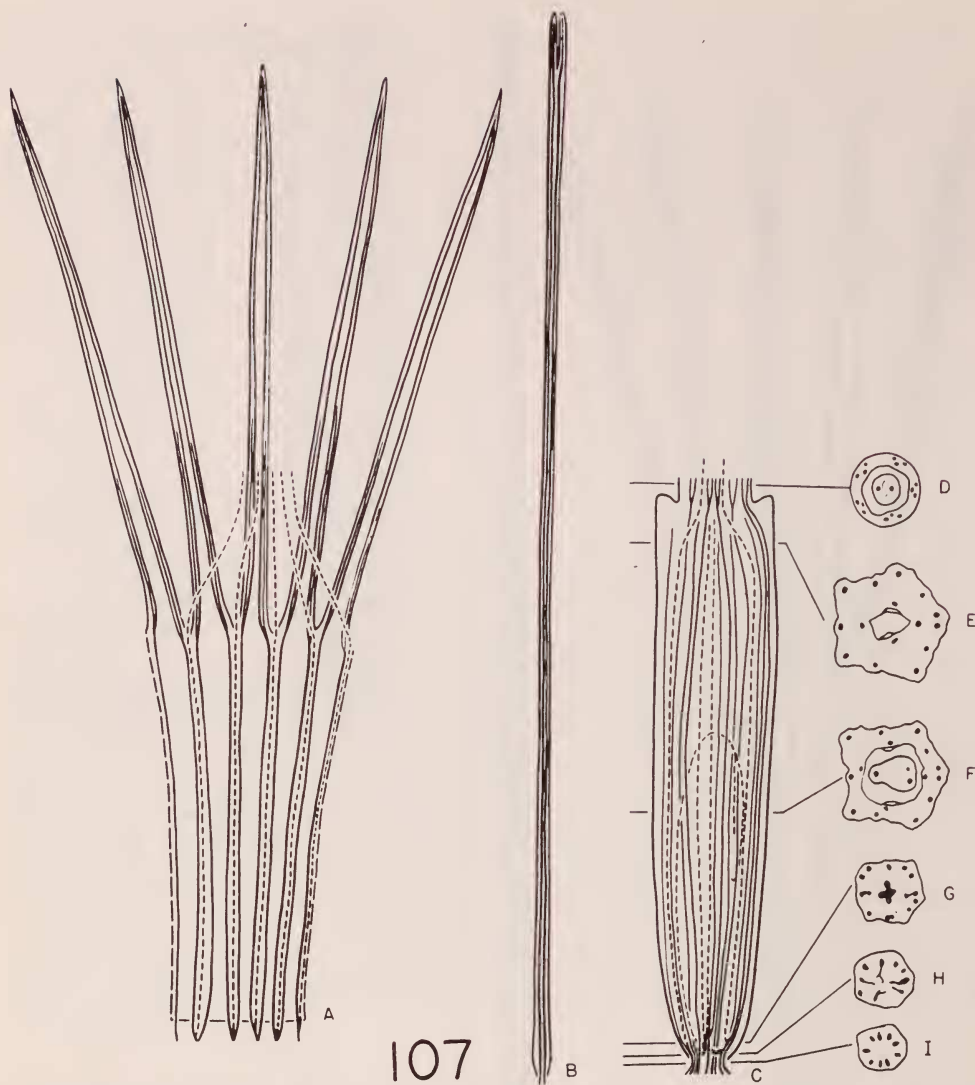


FIG. 107. *Stomatochaeta crassifolia* (Cowan & Wurdack 31162), portions of flower drawn to show venation. A, corolla; B, style; C, achene; D-I, sections of corolla base and achene at the levels indicated. A, B, $\times 4.5$; C-I, $\times 9$.

(fig. 106 D, F), but rather than extending to the base of the achene, they join exterior bundles at various points toward the top of the achene (fig. 106 D). Numerous other interior bundles, which terminate freely above, are present in the achene. Together with the ovule trace, these form, in the achene base, a plexus which separates into branches which join exterior bundles below. The ovule trace is unbranched. At the base of the achene, all of the exterior bundles unite into a single strand of vascular tissue which passes into the receptacle.

The floral vasculature of *Stiffia chrysantha* differs in several features from that of *Stenopadus*: union of laterals beneath the sinuses of the corolla; union of stylar traces with exterior achene wall bundles near the top of the achene; and union of all achene bundles at the base of the achene to form a single strand. Aside from these features, the venation is not unlike that of *Stenopadus*, an interesting similarity being the large number of interior bundles present in the

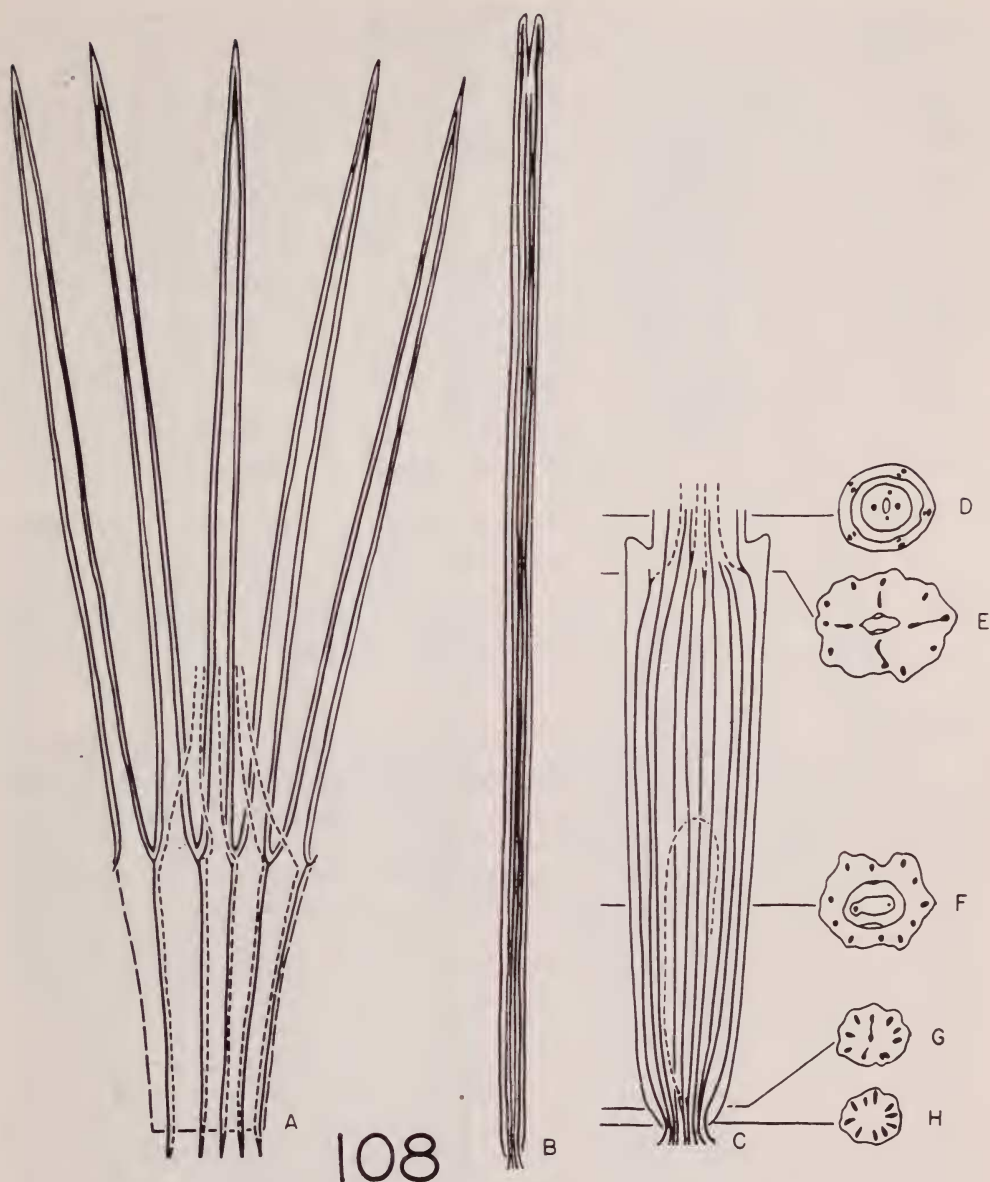


FIG. 108. *Chimantaea rupicola* (Steyermarck & Wurdack 748), portions of flower drawn to show venation. A, corolla; B, style; C, achene; D-H, sections of corolla base and achene at levels indicated. A, B, $\times 4.5$; C-H, $\times 9$.

achene. The venation of *Stiffitia uniflora* was found to be like that of *S. chrysantha*, with the exception that no median veins were found in the corolla of *S. uniflora*.

Stomatochaeta.

The other genera of Gochnatinae considered here, *Stomatochaeta*, *Chimantaea*, and *Quelchia*, have some features seen in *Stenopadus* and *Stiffitia* but are simpler in most features of floral vasculature. In the genus *Stomatochaeta*, *S. crassifolia* (fig. 107) shows a representative condition. The corollas (fig. 107A) have lateral veins which join at the tip of each lobe. In addition, subsidiary bundles, as in *Stenopadus kunhardtii*, branch from the laterals near the sinuses and extend for

a distance up the lobes, terminating freely. No median veins are present. In the top of the achene (fig. 107 C), the pairs of adjacent laterals unite. Xylem of stamen traces often unites with that of laterals in the summit of the achene. In addition to the five bundles in the achene connected directly with corolla bundles, five other exterior bundles are present (fig. 107 C). These run from a plexus at the achene top to the base of the achene. The style of *Stomatochaeta crassifolia* contains two bundles (fig. 107 B). These enter the achene as a dorsiventral pair of interior achene bundles (fig. 107 C). In addition, a lateral pair of interior bundles is present in the achene (see also fig. 107 E, F). Near the base of the achene, the dorsiventral interior bundles unite with nearby exterior bundles (fig. 107 G), while the lateral pair forms a plexus with the ovule traces. At a lower level, this plexus of vascular tissue is broken up into strands which join exterior bundles (fig. 107 H). A cylinder of bundles enters the receptacle (fig. 107 I). In the configuration of vasculature at the achene base, *Stomatochaeta crassifolia* shows considerable resemblance to species of *Stenopadus*, *S. cucullatus* for example. The ovule trace in the specimen examined was found to be dichotomously branched (fig. 107 C).

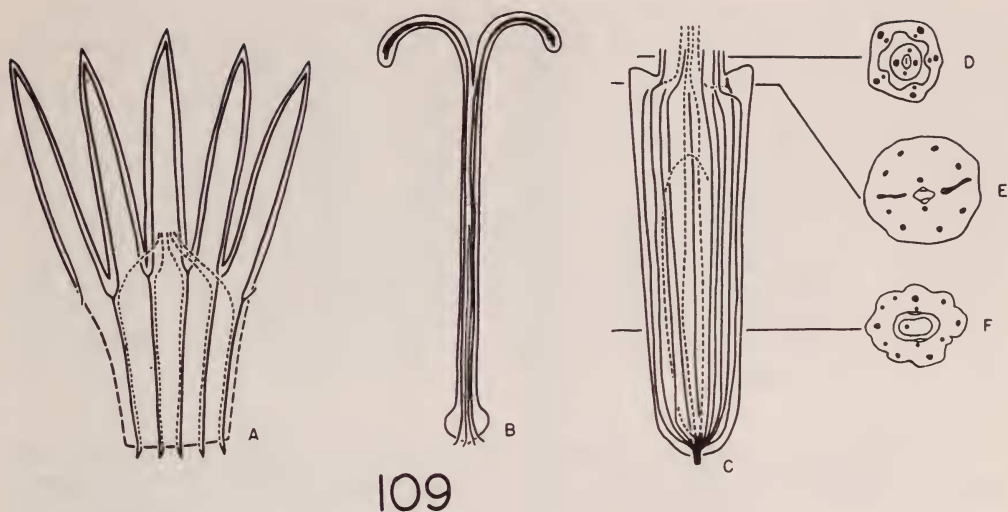
The other species of *Stomatochaeta* examined, *S. condensata*, *S. cylindrica*, and *S. cymbifolia*, agreed with the pattern described for *S. crassifolia* except that subsidiary bundles were not found in corollas of these species; they are often not present in *S. crassifolia*. Likewise, an unbranched ovule trace, seen in *S. crassifolia* in addition to the dichotomous condition, was seen in material of these species.

Chimantaea.

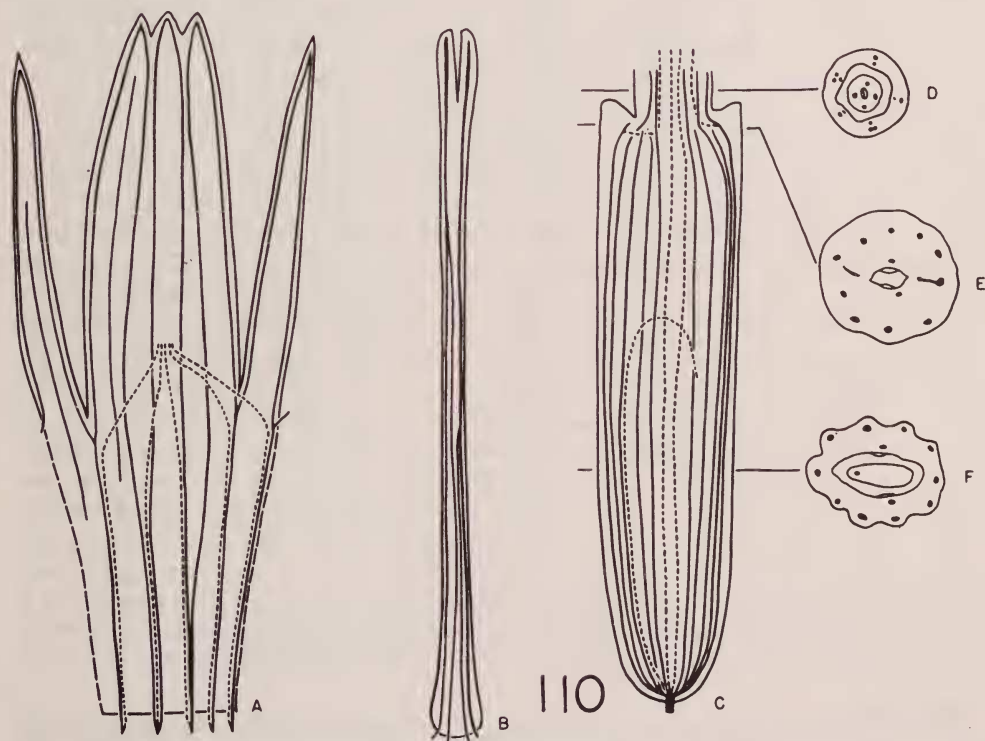
Although flowers of *Chimantaea* resemble those of *Stomatochaeta* closely in gross morphology and indument, they differ significantly in details of venation. Typical of the genus *Chimantaea* is *C. rupicola* (fig. 108). In the corollas of this species (fig. 108A), only lateral veins are present in the lobes. These fuse at the lobe apices; in addition, adjacent laterals fuse beneath the sinuses, a feature not seen in *Stomatochaeta*. Thus five corolla bundles, together with adjacent stamen traces (fig. 108D) enter the achene. Stamen traces join with these fused laterals in the achene top. In addition to the five corolline bundles, five other exterior bundles are usually found in the achene wall (fig. 108C). In the style (fig. 108B), the dorsiventral pair of bundles is present; a lateral pair of smaller bundles runs from just below the point of bifurcation of the stigmatic branches to the base of the style. The four (sometimes five) bundles of the style connect with exterior bundles only a short distance beneath the top of the achene (fig. 108C, E). Thus, in contrast to the taxa above, only exterior bundles are found in most of the length of the achene. The ovule trace is simple; at its base, its vascular supply divides to join exterior bundles (fig. 108G). At the base of the achene, as in *Stenopadus* and *Stomatochaeta*, a cylinder of vascular bundles (fig. 108H) enters the receptacle. Specimens of other species of *Chimantaea* (*C. lanocaulis*, *C. mirabilis*) showed a venation pattern identical to that described above for *C. rupicola*.

Quelchia.

A flower of *Quelchia cardonae* is seen in fig. 109. The corolla of this species (fig. 109A), like that of *Chimantaea rupicola*, exhibits a simplicity in structure which equals that found in the majority of Compositae. In the lobes, only lateral veins are found; these fuse beneath the sinuses and at the lobe tips. Thus five bundles and their associated stamen traces, which join with the corolla bundles in



109



110

FIG. 109. *Quelchia cardonae* (Pinkus 112), portions of flower drawn to show venation. A, corolla; B, style; C, achene; D-F, section of corolla base and achene at levels indicated A, B, $\times 4.5$; C-F, $\times 9$. FIG. 110. *Neblinaea promontorium* (Maguire, Wurdack & Bunting 37016), portions of flower drawn to show venation. A, corolla; B, style; C, achene; D-F, sections of corolla base and achene at levels indicated. A, B, $\times 4.5$, C-F, $\times 9$.

the achene top, enter the achene (fig. 109 C). Five other bundles, terminating upwardly at the achene top, are also present as exterior bundles in the achene. The style (fig. 109 B) contains the usual dorsiventral pair of bundles. At lower levels in the style, a pair of lateral bundles also is found, however. These four style bundles enter the achene (fig. 109 C); the dorsiventral pair unites with exterior bundles a short distance below the summit of the achene (fig. 109 E). The lateral pair continue down the achene as interior bundles (fig. 109 E, F). Near the base of the achene, the interior bundles fuse with the ovule trace; this grouping joins at the base of the achene a grouping formed from the exterior bundles. A single vascular strand connects the achene vascular tissue with that of the receptacle. Specimens examined of other species of *Quelchia*, *Q. conferta*, *Q. eriocaulon*, and *Q. × grandifolia*, were found to have a floral venation identical to that seen in *Q. cardonae*.

Neblinaea.

A number of similarities may be found between those genera of the present study having actinomorphic corollas (Gochnatinae) and those possessing bilabiate corollas (Gerberinae). Flowers of *Neblinaea* (fig. 110) are exemplary in this respect. Corollas of the only species, *N. promontorium* (fig. 110A), show lateral bundles in the two free lobes. It is of considerable interest to find that the lateral bundles of the three united lobes are not united as they are in bilabiate flowers of more advanced Mutisieae, such as are described below. The two pairs of adjacent "laterals" of this portion of the corolla fuse in the basal portion of the corolla, or in the achene top. Beneath the three sinuses beside the two lobes which are not united, however, the laterals fuse immediately below the sinuses. In addition to the full representation of lateral bundles in this corolla, median bundles are occasionally found either in the strap-shaped portion of the corolla or in the lobes which are separate. These median bundles terminate freely at both ends and extend only a short distance into the corolla tube. Stamen traces unite with corolla bundles in the top of the achene. As in the three preceding genera, ten bundles are present in the achene (fig. 110 C), five of these being additional to those connected to corolla bundles. As in *Quelchia*, four bundles are present in the style (fig. 110 B); the two lateral style bundles fuse with the dorsiventral pair at various points above the base. The achene structure is also identical to that of *Quelchia* in that the dorsiventral style bundles fuse with external achene wall bundles in the achene top (fig. 110 E), while the lateral style bundles continue into the achene as interior bundles accompanying the bands of stigmatoid tissue. The fusion of all bundles into a single strand of vascular tissue at the base of the achene is also like the condition found in *Quelchia*. The similarities of floral venation between *Quelchia* and *Neblinaea* are not cited here to suggest a close relationship between these genera. Rather, simplifications (as compared to genera described above) such as they show may occur independently.

Gongylolepis

The genus *Gongylolepis* is interesting to compare with *Neblinaea* in that although the flowers of most species are much larger than those of *Neblinaea*, their flowers do not have more complex venation; in fact, their pattern is often simpler than that just described. In *Gongylolepis bracteata* (fig. 111) the condition might be interpreted as basic for the genus, though it is not the most typical. In the corollas (fig. 111A) of this species lateral veins are present, fusing at the lobe-tips both in the two separate lobes and the three united lobes. The latter portion of the corolla exhibits a very interesting condition (mentioned

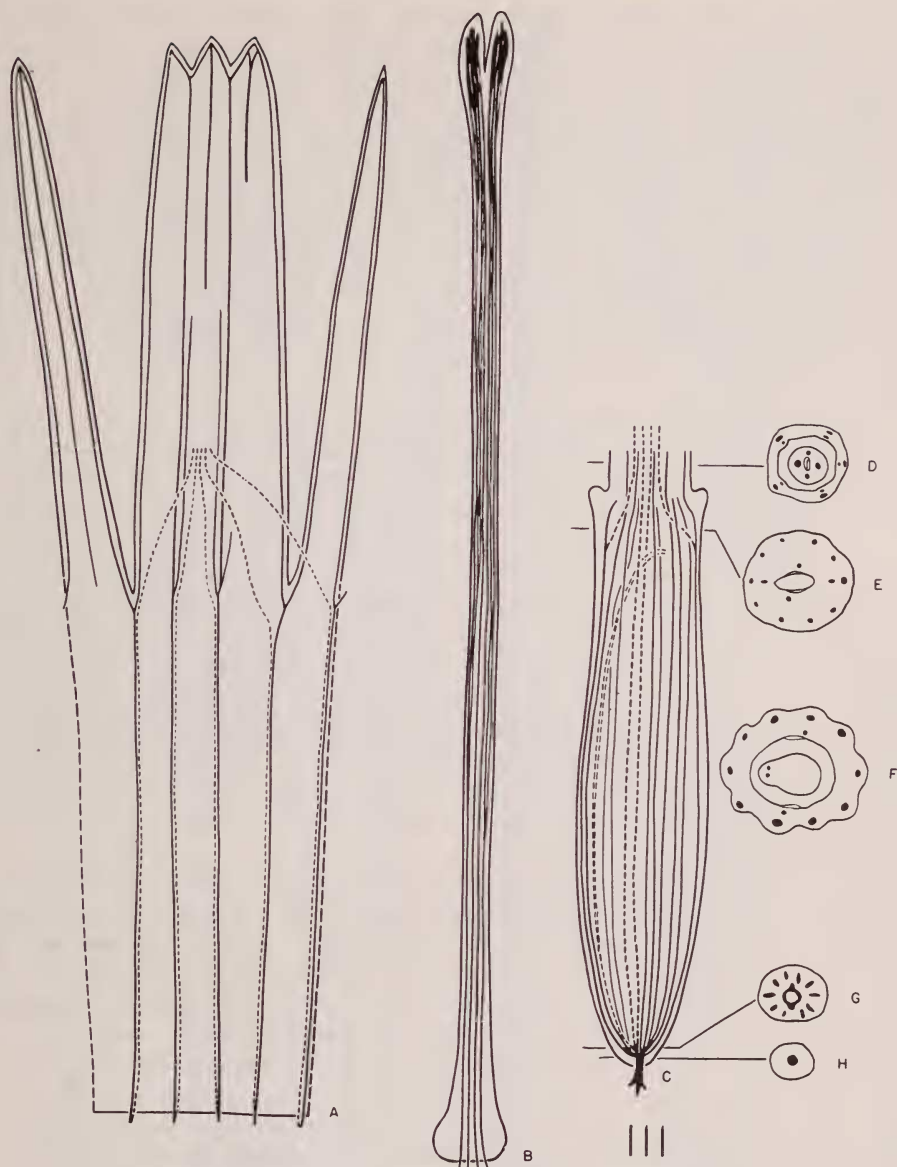


FIG. 111. *Gongylolepis bracteata* (Maguire 27560), portions of flower drawn to show venation. A, corolla; B, style; C, achene; D-H, sections of corolla base and achenes at levels indicated. A, B, $\times 4.5$; C-H, $\times 9$.

also in *Neblinaea*) in that although the laterals unite beneath the very short sinuses of this structure, freely terminating "lateral" bundles are also present further down, branching from the two central veins at the same level as the division of laterals below sinuses beside the two separate lobes. It is possible, therefore, to interpret this condition as a reflection of the vascular system of the actinomorphic corolla which is generally assumed to be ancestral to the zygomorphic condition. Further emphasizing a possibly primitive configuration, median bundles are often present for varying distances in the lobes of this species. In the tubular portion of the corolla, only five bundles, together with their associated stamen traces, are present. Stamen bundles unite with these

corolla bundles in the achene top. In addition to the corolline bundles, five more exterior bundles are found in the achene wall (fig. 111 C, F). The style of *Gongylolepis bracteata* (fig. 111 B) has four bundles at the base (fig. 111 D). In its upper portions, however, the bundles branch and anastomose, forming a more complex appearance; these groups of bundles are arranged on adaxial and abaxial sides of the style, and pass into the stigmatic branches. In the achene (fig. 111 C), the dorsiventral style bundles unite with exterior achene wall bundles on opposite sides of the achene. The lateral style bundles continue down the achene as interior bundles (see also fig. 111 F). Near the base of the achene these bundles unite with the ovule trace (fig. 111 G) to form a cylindrical plexus. Further down, this joins with the exterior bundles to form a single strand which connects with the receptacle. The ovule trace was found to be dual along most of its length.

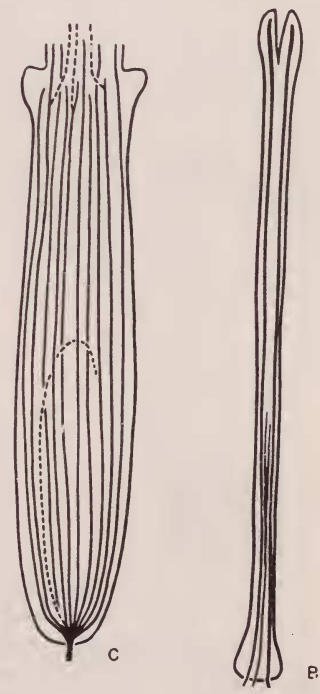
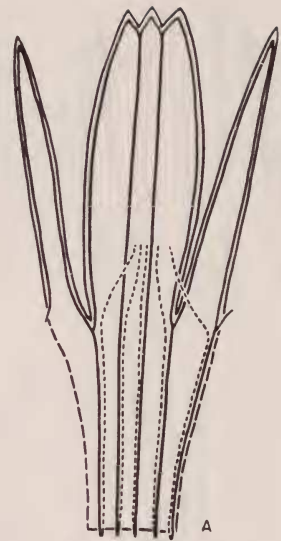
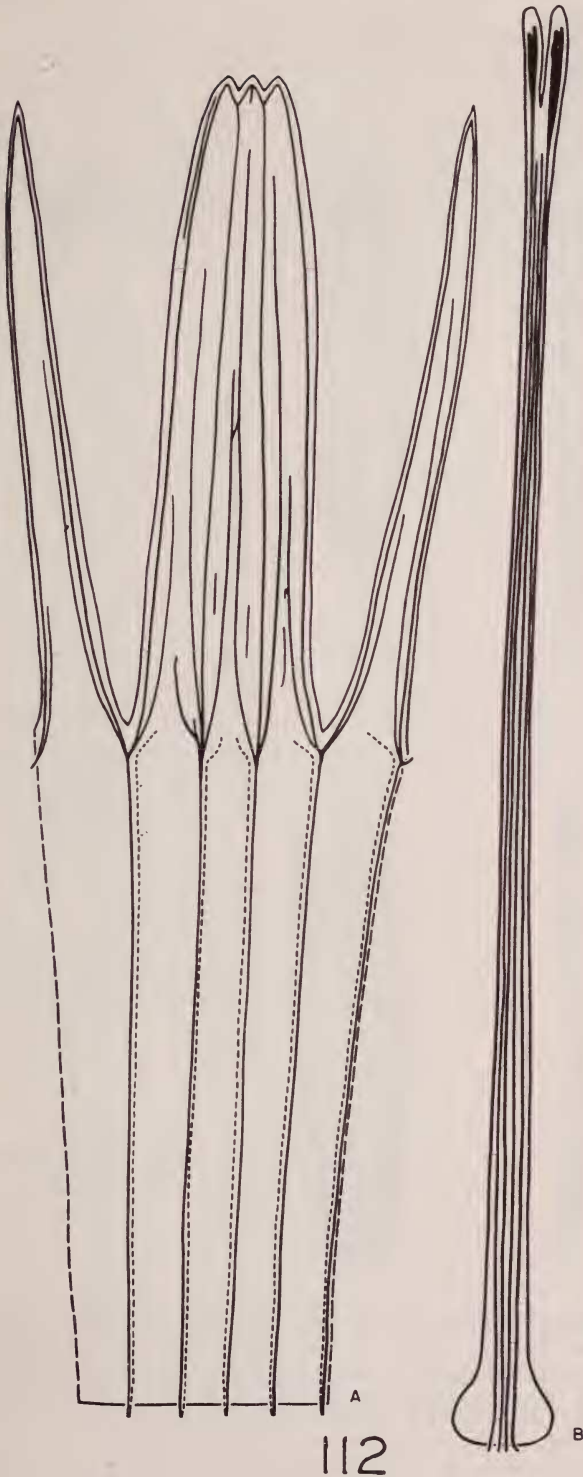
The drawing of *Gongylolepis pedunculata* (fig. 112) shows the only species of this genus studied in which a more complex corolla venation was found. In certain features it is like the condition in *G. bracteata*. A median vein, for example, is present for most of the length of the strap-like portion of the corolla. As in *G. bracteata*, two prominent veins from "laterals" beside the central two veins which run the length of this structure. These branch at the same level as the veins subtending sinuses beside the separate lobes. In addition, other veins branch off from the five main corolla-tube veins at this level. The shorter, freely terminating branches, unlike those of *Stenopadus kunhardtii* or *Stomatochaeta crassifolia*, are located inside, rather than outside, the true laterals. The style of *G. pedunculata* (fig. 112B) is simpler than that of *G. bracteata* in that only four bundles, all of which terminate freely, are found. The achene venation is like that of *G. bracteata*. The greater complexity of the corolla venation in *G. bracteata* may be correlated with the fact that this species has the largest flowers of the species of *Gongylolepis* studied.

The smallest-flowered species, *G. fruticosa*, (fig. 113), has been included for comparison. In the corolla of this species (fig. 113 A), the venation has reached the ultimate simplicity found in most zygomorphic corollas of Mutisieae. The laterals fuse directly beneath the sinuses, and no corolla veins are found in addition to the fused laterals. In the achene (fig. 113 C) the five corolline bundles are augmented, as in *G. bracteata*, by five more bundles, which terminate in the top of the achene. In the style of the flower of *G. fruticosa* studied (fig. 113 B), four bundles were present, though only three of these extended to the style base. In the achene (fig. 113 C), these were found to join achene wall bundles at a high level of the achene. Thus only exterior bundles were present in most of the length of the achene. A simple ovule trace is present; all the bundles of the achene unite at the achene base into a single strand of vascular tissue.

Despite the fact that their corollas are larger than those of *G. fruticosa*, the same corolla venation was seen in *G. huachamacari*, *G. martianus*, and *G. parvana*. The styles were all found to have four bundles; a pair of lateral interior bundles were usually not observed in achenes of these species, all the stylar bundles uniting with achene wall bundles at the summit of the achene. The ovule trace was often seen to be dual, at least in its upper portion.

Explanation of Figures 112-113

FIG. 112. *Gongylolepis pedunculata* (Cowan & Wurdack 31131), portions of flower drawn to show venation. A, corolla; B, style. $\times 4.5$. FIG. 113. *Gongylolepis fruticosa* (Steyermark & Wurdack 1136), portions of flower drawn to show venation: A, corolla; B, style; C, achene. A, B, $\times 4.5$; C, $\times 9$.



113

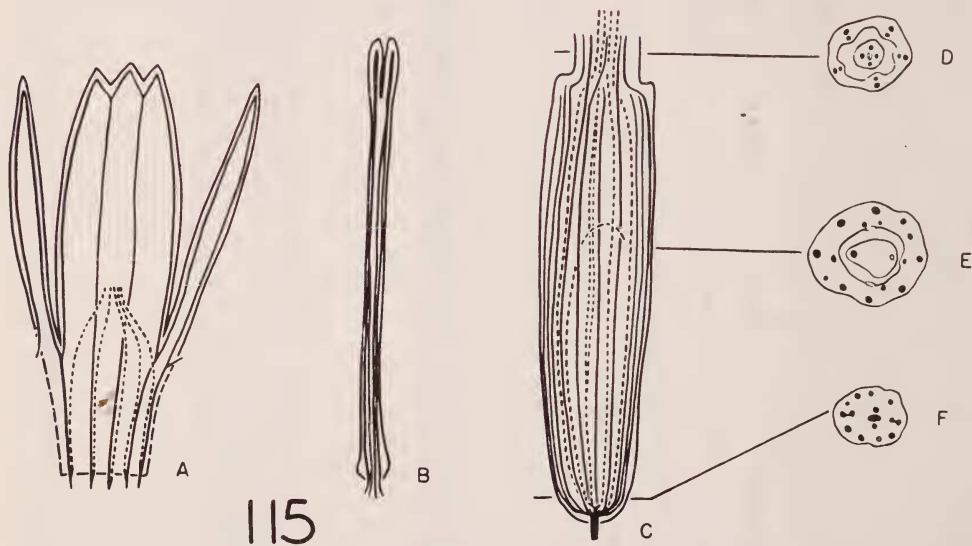
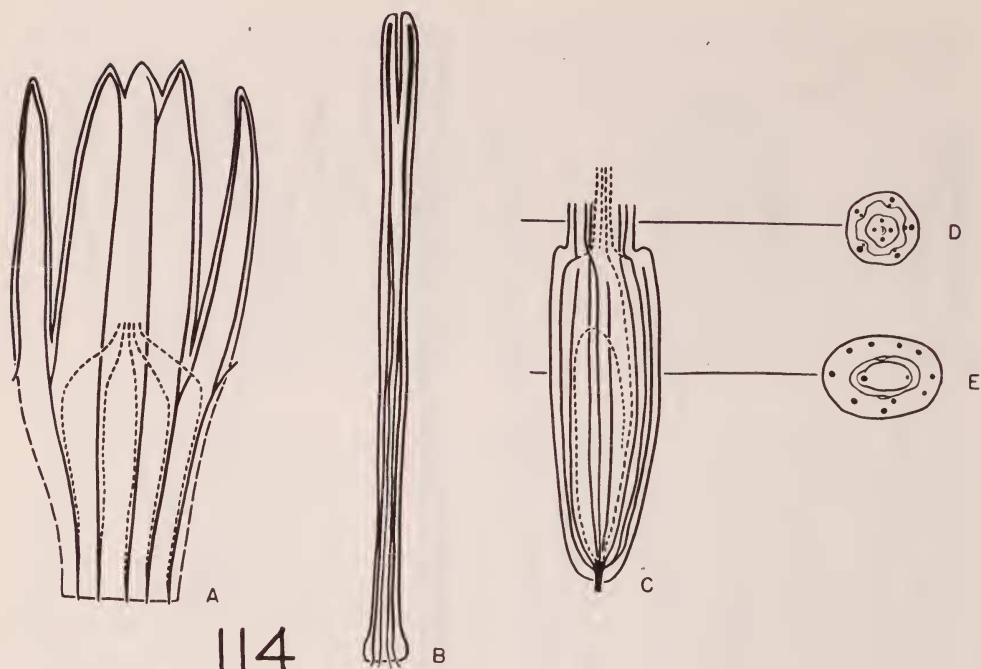


FIG. 114. *Duidaea tatei* (Steiermark 58204), portions of flower drawn to show venation. A, corolla; B, style; C, achene; D-E, sections of corolla base and achene at levels indicated. A, B, $\times 4.5$; C-E, $\times 9$. FIG. 115. *Achnopogon virgatus* (Steiermark & Wurdack 742), portions of flower drawn to show venation. A, corolla; B, style; C, achene; D-F, sections of corolla base and achene at levels indicated. A, B, $\times 4.5$; C-F, $\times 9$.

Duidaea.

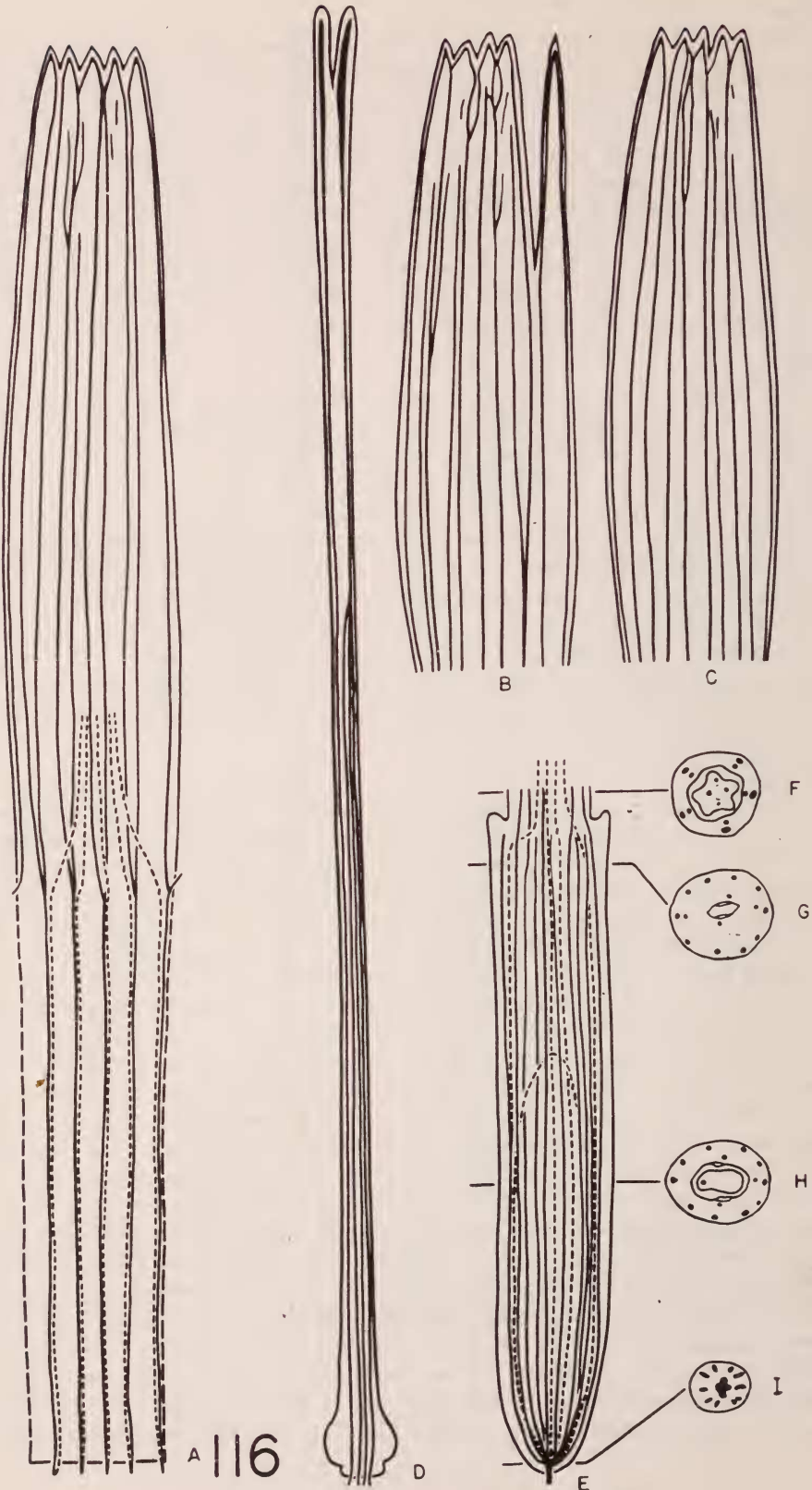
Portions of a flower of *Duidaea tatei* are shown in fig. 114. The corollas of this species (fig. 114A) exhibit the simplified type described above for *Gongylolepis fruticosa*. Although the five corolla-tube veins continue into the achene, fewer than five additional exterior bundles may be present (fig. 114 C, E). Stamen traces unite with the associated corolla veins in the corolla-tube. In the style (fig. 114 B) four bundles are present. The dorsiventral pair of these unites with achene wall bundles in the achene summit. In the flower studied, only one of the lateral bundles was seen to form an interior bundle in its extension into the achene. A simple ovule trace is present, and all of the bundles in the achene unite at the base into a single strand. *Duidaea pinifolia* was found to have a vasculature pattern like that shown for *D. tatei*.

Achnopogon.

The corolla of the monotypic genus *Achnopogon* (fig. 115 A), like that of *Duidaea*, has a simplified venation. In the achene, the full complement of ten bundles is present, half of them continuing upwards into the corolla-tube. Stamen traces unite with the corolla-tube bundles in the achene top. In the style of *Achnopogon* (fig. 115 B), as in that of *Duidaea tatei*, four bundles are present, the lateral two uniting with the dorsiventral pair at various points along the length of the style. Rather than joining with exterior achene wall bundles, however, all four continue into the achene as interior bundles. (fig. 115 E). In the achene illustrated, one of the lateral interior bundles is double along part of its extent. At the base of the achene, the dorsiventral pair of interior bundles unites with nearby exterior bundles, while the lateral interior bundles and the ovule trace unite as a central plexus; this plexus joins, further down, with the single strand formed by the union of all of the exterior bundles.

Glossarion.

Flowers of the monotypic genus *Glossarion* (fig. 116) are of particular interest in that they are ligulate in form, all the lobes being united except at the tips (fig. 116 A-C). Although the lobes are histologically united, the vascular anatomy suggests that the corolla form is basically actinomorphic, with some degree of modification. As the corolla in figure 116 A shows, some of the lateral veins unite beneath the short sinuses at the "ligule" tip. It seems significant, however, that each of the five veins of the corolla-tube divides into two laterals at the same level as the vein beneath the single deep sinus in the corolla. Portions of two other corollas are shown (fig. 116 B, C) to indicate the variation in venation at the corolla tip. In each of these, however, ten laterals are present in the more basal portion. Occasionally one of the outer lobes may be separate for a short distance (fig. 116 B). The vascular pattern of the corolla, then, shows little modification from an actinomorphic form, although the tissues between these lobes are continuous. This is a stage in union of corolla lobes beyond that found in *Fitchia* (Carlquist 1957b), where sinuses are histologically formed between the lobes, although only the adaxial sinus usually opens during anthesis. Stamen traces unite with their associated corolla bundles in the achene top. In addition to the five exterior bundles, which continue into the corolla, five additional bundles, terminating at the achene summit, form the complement of ten exterior achene bundles (fig. 116 E). The style of *Glossarion* (fig. 116 D) contains four bundles, uniting to two above. These four bundles continue downward into the achene as interior bundles. Occasionally one of the dorsiventral interior bundles may unite with a nearby exterior bundle (fig. 116 H). The lateral pair, however,



follow the bands of stigmatoid tissue to the base of the achene, uniting with the ovule trace (fig. 116 I). A single vascular strand results from the union of all of the bundles at the achene base. The ovule trace is simple.

DISCUSSION

The floral vascular patterns given above serve as additional taxonomic criteria in separating the genera of Guayana Mutisieae investigated in the present study. The segregation of *Stomatochaeta* and *Chimantaea* from *Stenopadus* is justified by the differences found in floral venation among these genera. *Quelchia* is distinct from these genera in certain details, though similar in most respects. Within the Gerberinae studied in this paper, simplification from the patterns seen in *Neblianaea* and *Gongylolepis bracteata* is seen in other species of *Gongylolepis*, such as *G. fruticosa*, *Duidaea*, and *Achnopogon*. This is in accord with the suggestion of Maguire (1956; and Maguire & Wurdack 1957) that these latter taxa are advanced derivations from a gongylolepoid stock. The anomalous corolla form of the genus *Glossarion* is clarified by study of the underlying venation pattern. As stated by Maguire and Wurdack (1957), this ligulate corolla form seems to be a modification of a basically actinomorphic form.

The differences in floral venation described above are significant in that they suggest evolutionary trends within the Mutisieae. As indicated by Maguire (1956), the genera of Guayana Mutisieae considered here represent not only a geographical assemblage of genera, but also a series of primitive forms in the two subtribes concerned, Gochnatinae and Gerberinae. Since the Gochnatinae are generally considered to contain the most primitive features to be found in the Mutisieae as a whole, the characters of Guayana Gochnatinae become of interest in attempting to deduce primitive structural features in Compositae at large. The introduction of *Stiffitia*, a member of Gochnatinae occurring outside the limits of Guayana, into this study was intended to demonstrate the most primitive floral venation pattern which could be found in non-Guayana Gochnatinae.

It seems apparent that the vascular characters described above cannot be arranged in a single line from complex to simple. In such species as *Stenopadus kunhardtii* and *Gongylolepis pedunculata*, it seems probable that increase in number of vascular bundles from the basic condition has taken place. However, the following possible sequences in the evolution of the Mutisioid flower may be suggested:

(1) Corolla. Median veins in corolla-lobes of Mutisieae have been regarded as primitive in the genus *Anaethaphia* (currently treated as *Gochnatia*) by Koch (1930a); a similar interpretation was given from *Hesperomannia* (Carlquist 1957a). The progressive loss of median bundles may be regarded as an indication of advance. It may be that the close relation between stamen traces and lateral bundles provides an explanation for the discarding of median, rather than lateral bundles in the vascular simplification of the composite flower. It seems likely that separate pairs of laterals in the corolla-tube have preceded united lateral bundles. In some *Stenopadus* species considered here such adjacent lateral bundles were often not united even in their downward extension into the achene.

Explanation of Figure 116

FIG. 116. *Glossarion rhodanthum* (Maguire, Wurdack & Bunting 37190), portions of flowers drawn to show venation. A, corolla; B, C, upper portions of corollas of other flowers; D, style; E, achene; F-I, sections of corolla base and achene at levels indicated. A-D, $\times 4.5$; E-I, $\times 9$.

It is difficult at present to suggest whether the subsidiary bundles, such as occur in corollas of *Stenopadus kunhardtii*, *S. stipitatus*, and *Stomatochaeta crassifolia*, represent features of a primitive venation pattern or are secondary additions.

In the zygomorphic corolla of Geberinae, union of the abaxial three lobes has involved the reduction from pairs of laterals to single bundles in the united portion. Stages in this simplification are offered by *Neblinaea* and two species of *Gongylolepis*. The final simplified form was described by Koch (1930a,b) in *Perezia microcephala* and *Mutisia taraxacifolia*, although she suggests no stages in its origin.

The genus *Glossarion* appears to represent a special case in which the lobes of an actinomorphic flower have united without any great alteration of the vascular system.

(2) Achene. In the achenes of *Stenopadus kunhardtii*, *S. stipitatus*, and *S. cucullatus*, adjacent laterals continue downward without fusing (although a vascular plexus often interconnects many of these bundles at the achene top). In most of the taxa considered here, however, the pairs of laterals unite in the achene top and continue downward as five of the exterior achene wall bundles. Ten bundles are very commonly present in flowers showing this condition, and the additional five bundles are accounted for by continuation of median corolla veins into the achene, as in *Stenopadus campestris*. Very often, however, median bundles are not present in the corolla, or present only as isolated portions in the lobes. The presence of additional bundles in the achene may then be accounted for by preferential retention of bundles in the achene, although their upward extension as median traces has been lost phyletically in the corolla. Koch (1930b) described the achene anatomy for Mutisieae only in an advanced form, *Mutisia taraxacifolia*, in which the bundle number in the achene was reduced to five. The presence of ten bundles in achenes of Mutisieae has been described previously by Giroux (1937) in *Dicoma tomentosa*.

The reader will have noted that a difference occurs between the genera *Stenopadus*, *Stomatochaeta*, and *Chimantaea*, and the remaining genera in this study in the configuration of bundles at the achene base. In the three genera named a cylinder of independent bundles enters the receptacle, while in the others all the achene bundles fuse to a single strand. Snow (1945) has asked, quite appropriately, why there should be a single vein supplying the base of the achene in the Compositae she investigated, rather than a floral stele consisting of several bundles, such as is found in flowers of other families. This question can be answered by saying that consistent reduction in the vascularization of the composite flower has resulted in this simplified situation, but the presence of an actual cylinder of bundles in the taxa named shows that such a condition is indeed present in primitive Compositae.

Apparently the pappus of the Mutisieae investigated here is advanced compared with that of primitive Heliantheae, and although many of the pappus bristles are quite thick and contain some degree of differentiation among cells in their interior, there are no vascular elements present in the pappus. However, the fact that phloem strands may be seen to lead out to the pappus base in several of the genera (particularly *Glossarion* and *Gongylolepis*) could be used in support of the idea that the pappus was primitively a calycine structure more nearly like that shown by certain primitive Heliantheae.

(3) Style and carpels. Because in flowers of Mutisieae or other Compositae described heretofore only a single circle of bundles has been found in the achene,

no suggestions have been made previously concerning the primitive carpellary structure in Compositae. One might expect that the ancestral condition for Compositae would have an interior set of bundles, representing carpellary vascular supply, as well as an exterior set representing that of perianth parts, as well as of the stamens. As the descriptions in the main body of this paper indicate, this is indeed the case in the majority of these Guayana Mutisieae. Furthermore, it is interesting that many of these genera show a characteristic grouping of these bundles at the base of the achene. The dorsiventral pair—representing the main stylar traces, and homologous to median traces of the carpels supposed to have been primitively present in Compositae by Eichler (1875)—often join exterior bundles, which form a plexus at the base of the ovule trace. The large number of lateral interior bundles in some of the taxa considered here (*Stenopadus kunhardtii*, for example) may represent a secondary increase in the number of such bundles, but the frequent presence of a lateral pair as well as a dorsiventral pair suggests that at least these four may have been present primitively.

A functional correlation might explain the fact that lateral interior bundles often closely accompany the two bands of stigmatoid tissue on the interior of the achene wall. The double nature of these lateral interior bundles beside stigmatoid tissue in several of the taxa described here (see *Stenopadus cucullatus*, for example) may be a further suggestion of a two-carpellate condition. Some lateral bundles often develop phloem only, suggesting (as in filaments of many Compositae) that loss of xylem precedes loss of phloem in the progressive reduction of vascular tissue.

In the Heliantheae, the writer (Carlquist 1957b) proposed that the presence of four bundles in the style represents a primitive condition. The connection of the style bundles to interior, or carpellary, bundles in the achenes of Mutisieae would seem to substantiate this suggestion. Differential loss of vascular tissue in different parts of the flower could explain why lateral carpellary bundles may be present in some of the taxa studied here (*Stenopadus*, for example) without lateral style bundles. *Stenopadus cucullatus* would represent a species in which this reduction has not occurred.

Also on the basis of study of primitive Heliantheae, the writer considered that a dichotomous ovule trace might be a primitive character, and that ancestrally two ovules may have been present. The frequent occurrence of a dichotomous ovule trace in the Mutisieae studied here would seem to offer an additional instance of this condition. The elaborately branched ovule trace of *Stenopadus kunhardtii*, however, is probably best interpreted as a secondary increase in the vascularization of the ovule.

The vascular patterns described above would seem to require an explanation in evolutionary terms, and other studies are desirable in supplying a comprehensive picture of evolution in the primitive Compositae. The writer wishes to emphasize the agreement between data from gross morphology assembled by Maguire and his colleagues and the anatomical descriptions given here. Further studies, particularly on stem and wood anatomy, are planned to aid in the development of a thorough understanding of this group.

CLAREMONT GRADUATE SCHOOL
RANCHO SANTA ANA BOTANIC GARDEN
CLAREMONT, CALIFORNIA

Literature cited

- Carlquist, Sherwin. 1957a. Systematic anatomy of *Hesperomannia*. Pac. Sci. [ined.]
- . 1957b. The genus *Fitchia*, an anatomical study in the primitive Heliantheae. Univ. Calif. Publ. Bot. [ined.]
- Erdtman, G. 1952. Pollen morphology and plant taxonomy. Chronica Botanica, Waltham, Mass.
- Eichler, A. W. 1875. Blüthendiagramme. Wilhelm Engelmann, Leipzig.
- Faegri, K. & Iversen, J. 1950. Textbook of modern pollen analysis. Ejnar Munksgaard, Copenhagen.
- Frei, Eva. 1955. Die Innervierung des floralen Nektarien dikotylen Pflanzenfamilien. Ber. Schweiz. Bot. Ges. 65: 60-114.
- Giroux, M. 1937. Morphologie florale et carpologie de *Dicoma tomentosa* Cass. Bull. Soc. Bot. Fr. 84: 700-713.
- Johansen, D. A. 1940. Plant microtechnique. McGraw Hill, New York.
- Koch, Minna. 1930a. Studies in the anatomy and morphology of the composite flower. I. The corolla. Am. Jour. Bot. 17:938-952.
- . 1930b. Studies in the anatomy and morphology of the composite flower. II. The corollas of the Heliantheae and Mutisieae. Am. Jour. Bot. 17:995-1010.
- Maguire, Bassett. 1956. Distribution, endemism and evolution patterns among Compositae of the Guayana Highland of Venezuela. Proc. Am. Philos. Soc. 100:467-475.
- Maguire, Bassett, Cowan, Richard S. & Wurdack, John J. 1953. The botany of the Guayana Highland. Mem. N. Y. Bot. Gard. 8:87-160.
- Maguire, Bassett & Wurdack, John J. 1957. Botany of the Guayana Highland—Part II. Mem. N. Y. Bot. Gard. 9:235-392.
- Maguire, Bassett, Steyermark, Julian A. & Wurdack, John J. 1957. Botany of the Chimantá Massif.—I. Mem. N. Y. Bot. Gard. 9:393-439.
- Snow, Edna. 1945. Floral morphology of *Chrysothamnus nauseosus*. Bot. Gaz. 106:451-462.
- Wodehouse, Roger P. 1929a. Pollen grains in the identification and classification of plants. III. The Nassauvinae. Bull. Torrey Club 56:123-138.
- . 1929b. Pollen grains in the identification and classification of plants. IV. The Mutisieae. Am. Jour. Bot. 16:297-313.